SOIL SEED BANKS, HETEROGENEITY, AND PLANT COMMUNITY ASSEMBLY FOLLOWING DISTURBANCE BY FIRE AND LOGGING IN INTERIOR DOUGLAS-FIR FORESTS

by

KAELI ELIZABETH STARK

B.Sc., The University of Guelph, 2002

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF,

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

(Botany)

THE UNIVERSITY OF BRITISH COLUMBIA

September 2005

ABSTRACT

Soil seed banks and establishing plant communities were examined in Interior Douglas-fir forests within the first year following low severity fire, high severity fire, and logging, as well as on five-year-old burned sites and ten-year-old logged sites, and undisturbed sites in the vicinity. The effects of different types of disturbance on the regenerative potential and spatial structure of forest plant communities were compared using univariate and multivariate analytical methods. On the one-year-old severely burned sites, the species composition of the seed bank and establishing vegetation were similar because a high proportion of the establishing vegetation of was of seed origin; however, differences between seed bank and vegetation species composition were detected for the one-year-old lightly burned and logged sites, and the undisturbed reference sites. Whereas the frequency of seed-origin plants in the establishing vegetation decreased in the order lightly burned > severely burned > logged, the frequency of root-derived plants did not differ across disturbance types. The low frequency of seed-derived plants, particularly conifer seedlings, on logged sites poses concerns for the initial recovery of vegetation following logging; nonetheless, the lack of significant differences in species composition between five-year-old burned sites, ten-year-old logged sites and their corresponding undisturbed sites suggests that vegetation recovery occurs with time. Considerable spatial variation in seed bank and vegetation species composition occurred both among and within the one-year-old sites. In general, disturbed sites exhibited less among-site heterogeneity than undisturbed sites, likely because of homogenizing, post-disturbance seed rain events; however, within-site variability in seed bank species assemblages was greatest on severely burned and logged sites. Species-area curves and jackknife estimates indicated that 63-83% of species actually present were detected in seed bank sampling. The results presented in this thesis provide forest managers with deeper insights into the interaction between disturbance and re-vegetation processes in Interior Douglas-fir forests.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

1. INTRODUCTION

1.1 Disturbance and community assembly

Fires of varying frequency and severity have occurred in northern coniferous forest ecosystems for thousands of years (Tolonen 1983), and different strategies for persistence and regeneration have been identified for the plant species occurring in such disturbance-prone habitats (Rowe 1983; Agee 1993; Pausas et al. 2004). Specifically, the species that are often most successful during the period of recruitment immediately following fire are those able to recruit from seeds (Rowe 1983; Clark and Wilson 1994) or regenerative vegetative structures (McLean 1969; Ingersoll and Wilson 1990; Whittle et al. 1997; Greene et al. 1999; Wang 2003) stored *in situ*, species able to disperse efficiently and recruit on a mineral soil seedbed (Chrosciewicz 1974; Zasada et al. 1983; Parker et al. 1997; Arseneault 2001), and species with thick, insulative bark (Precht et al. 1973; Peterson and Ryan 1986; Ryan and Reinhardt 1988; Agee 1993).

As fire intensity increases, the probability of lethal heat penetration through insulative bark structures increases and the persistence of woody individuals in the post-fire environment decreases (Agee 1993). Similarly, as fire severity and associated soil consumption increase, the contribution of structures stored *in situ* (e.g. buried seeds and rhizomes) decreases, and the contribution of structures of *ex situ* origin (e.g. wind and animal dispersed seeds) necessarily increases (Schimmel and Granström 1996). While the pre-disturbance soil seed bank is often characterized and cited for its role in providing species for post-disturbance colonization (Moore and Wein 1977; Morgan and Neuenschwander 1988; Fyles 1989), the actual contribution of the soil seed bank to establishing plant communities depends not only on which species are able to survive the disturbance, but also on their responses to modified, post-disturbance abiotic conditions (Thomas and Wein 1990; Baskin and Baskin 1998). The few studies that have assessed the *actual* contributions of this *potential* seed-derived community to the post-disturbance vegetation indicate that seed bank contributions are variable and system-dependent, and, thus, require further study (Beatty 1991; Yearsley 1993; Hyatt 1999; Lee 2004). The relationship between soil seed banks and establishing vegetation will be examined in this study.

Logging has become an increasingly common disturbance in many northern coniferous forest ecosystems since the expansion of European settlement in the 19th century. Although logging practices that are designed to mimic the natural disturbance regime of the target system are expected to be most sustainable (Duchesne 1994), the similarity between current harvesting practices and natural disturbance regimes has been called into question (e.g. Whittle et al. 1997). In his Initial Floristic Composition (IFC) hypothesis, Egler (1954) argued that the majority of species that will eventually gain dominance on a site are present immediately following disturbance. Therefore, if there are differences in seed bank or vegetation species composition immediately following different types of disturbance, it is likely that these differences will persist as succession

proceeds (e.g. Timoney and Peterson 1996). In order to predict the long-term trajectories of vegetation development following fire and logging, an understanding of plant community assembly during the initial, post-disturbance phase is required.

1.2 Heterogeneity and the soil seed bank

Published descriptions of soil seed banks date back to at least the mid-1800s (e.g. Salter 1857). Seed density (Kellman 1974) and seed bank species composition (Whipple 1978; Kellman 1970; Granström 1982; Kramer and Johnson 1987), seed viability (Telewski and Zeevaart 2002; Schafer and Kotanen 2003) and seed dormancy (Pratt et al. 1984; Baskin and Baskin 1998), seed banks in the context of succession (Oosting and Humphreys 1940; Livingston and Allessio 1968; Donelan and Thompson 1980) and disturbance (Olmsted and Curtis 1947; Moore and Wein 1977; Morgan and Neuenschwander 1988; Beatty 1991; McGee and Feller 1993; Qi and Scarratt 1998), as well as the methods used to quantify soil seed banks (Kropáč 1966; Roberts 1981; Forcella 1984; Bigwood and Inouye 1988; Gross 1990; Brown 1992; Ter Heerdt et al. 1996) have been examined in detail in many different types of ecosystem. Despite these numerous investigations, our understanding of seed bank structure and function is incomplete (e.g. Warr et al. 1993; Clark et al. 1999). In particular, soil seed banks can vary in both space and time (Thompson and Grime 1979; Henderson et al. 1988; Coffin and Lauenroth 1989; Owen et al. 2001), but the extent and importance of this variation is unknown (Clark et al. 1999). Many accounts of seed bank spatial structure have focused on vertical patterns in the soil profile (Moore and Wein 1977; Granström 1982; Kramer and Johnson 1987; McGee and Feller 1993; Qi and Scarratt 1998; Staniforth et al. 1998); horizontal spatial structure has received less attention (Clark et al. 1999). The spatial arrangement of seeds in the seed bank, and the proximity of seeds to their neighbours can affect seed germination and seedling establishment events (Inouye 1980; Murray 1998), which, in turn, can determine trends in plant community structure.

Our perception of spatial heterogeneity in soil seed bank structure is a function of the spatial scale of sample collection, so it follows that ecologically meaningful descriptions of seed bank heterogeneity should use samples collected from ecologically relevant spatial scales. Many studies of seed bank spatial structure have occurred at spatial scales of less than 10 m x 10 m within one site (e.g. grassland: Thompson 1986; Henderson et al. 1988; Coffin and Lauenroth 1989; old field: Bigwood and Inouye 1988; sand dune: Lortie and Turkington 2002; temperate forest: Olano et al. 2002; arable field: Shaukat and Siddiqui 2004). While these fine spatial scales were appropriate to answer the questions of interest, when one is concerned with landscape-level issues such as a characterization of the seed bank of a given vegetation type, or the potential for regeneration from seed banks following stand-level disturbance, sampling from multiple sites over a larger geographic area is necessary.

1.3 Disturbance and seed banks in Interior Douglas-fir forests

During the summer of 2003, wildfires burned more than 80 000 hectares of forest in the interior of British Columbia. Fires ranged from low severity surface scorches to high severity canopy fires, and many stands of trees in the Interior Douglas-fir forest zone were burned. Because this type of forest is also continually subject to logging, it was considered appropriate for a study comparing the effects of fire and logging on soil seed banks and the subsequent recovering vegetation communities. The main focus of this study was on the species present in seed bank and vegetation communities in the first post-disturbance growing season because they form the basis for future vegetation development (Egler 1954). Sites that had burned in 1998 (five years prior to sampling) and sites that were logged in 1993 (ten years prior to sampling) were also examined to determine whether any of the trends detected in the first growing season were persistent in this time frame.

1.4 Thesis outline and objectives

This thesis is organized such that Chapter 1 gives an introduction and brief overview of the seed bank literature, and Chapter 2 outlines the overall study design including field sampling, greenhouse protocol, and methods of data analysis. Chapters 3 and 4 are the main data chapters, and they describe the effects of disturbance on seed banks and community assembly (Chapter 3), and spatial seed bank structure and vegetation heterogeneity in relation to disturbance (Chapter 4). General conclusions are drawn in Chapter 5.

The objectives of Chapter 3 are to:

(i) determine the number of seeds, the number of species, and the species composition of soil seed banks disturbed by fire or logging less than one year prior to sampling,

(ii) compare the species composition of this *potential* seed-derived community to that of the *actual* plant communities that established in the field during the first post-disturbance growing season, and

(iii) compare seed bank and vegetation communities on sites disturbed five and ten years prior to sampling by fire and logging (respecitvely) to those on neighbouring undisturbed sites.

The objectives of Chapter 4 are to:

(i) determine the extent to which the species composition of soil seed banks on undisturbed sites varied at coarse (among-site) and fine (within-site) spatial scales,

(ii) describe how among- and within-site heterogeneity in seed bank and vegetation species composition is affected by disturbance, and

(iii) determine the effectiveness of the sampling design used in this study for estimating the total number of species in soil seed banks subject to different types of disturbance.

2. METHODS

2.1 Study area

This study was carried out in the Interior Douglas-fir (IDF) forest zone near Kamloops (51°45' N, 120°20' W) in south-central British Columbia (BC). Mean annual precipitation ranges from 300 to 850 mm, and the climate is characterized by warm, dry summers and cool winters with low to moderate snowfall (Lloyd et al. 1990). The dominant canopy species in the IDF is Douglas-fir (*Pseudotsuga menziesii*), but lodgepole pine (*Pinus contorta*), hybrid white spruce (*Picea glauca x engelmannii*), ponderosa pine (*Pinus ponderosa*), trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) are also important constituents of the community (Lloyd et al. 1990). Characteristic understory species include *Arctostaphylos uva-ursi*, *Arnica cordifolia*, *Calamagrostis rubescens*, *Linnaea borealis*, *Paxistima myrsinites*, *Shepherdia canadensis*, and *Spiraea betulifolia*. Soils are generally Orthic or Dark Gray Luvisols, and Eutric or Dystric Brunisols with a medium to rich nutrient regime. Humus forms are usually 2-5 cm thick Hemimors and Mormoders (Lloyd et al. 1990).

Based on vegetation and environmental characteristics, the IDF zone can be divided into seven subzones, two of which were sampled for this study - IDFxh and IDFdk. The IDFxh subzone occurs at elevations between 400 and 1250 m and it is typically hotter and drier than the IDFdk subzone, which occurs at higher elevations (between 600 and 1460 m; Lloyd et al. 1990). The dominant tree species in both subzones is Douglas-fir, with ponderosa pine as a common associate on the drier, IDFxh sites, and lodgepole pine on the more moist, IDFdk sites (Lloyd et al. 1990).

Interior Douglas-fir forests are continually subject to disturbance from fire, wind-throw, outbreaks of defoliating insects, livestock grazing, and logging (Huggard et al. 2005). The fire regime in the IDF forest zone is classified as *mixed-severity*, meaning that low, moderate, and high severity fires, often occurring in close spatial proximity, are common. The result is a structurally complex forest made up of patches of varying size, shape, and age (Arsenault and Klenner 2004). Although lower volume, selective harvesting is arguably more ecologically sustainable than higher volume, partial or clear cutting in this type of forest, for economic reasons, the latter is more often implemented than the former in IDF forests (Huggard et al. 2005). The three types of disturbance sampled for this study were: low severity fire, high severity fire (meant to represent the two ends of the natural fire severity gradient in this forest type; Arsenault and Klenner 2004), and logging (in harvested areas ≥ 1.5 ha in size). Fire severity on sites that had been burned less than one growing season prior to sampling was determined using a *post hoc* classification scheme based on the extent of forest floor charring and resultant exposure of mineral soil (Ryan and Noste 1985).

2.2 Field sampling

While the main focus of the study was on seed bank and vegetation responses to disturbance by low severity fire (light burn: LB-1), high severity fire (severe burn: SB-1), and logging (clearcut: CC-1) during the first post-disturbance growing season, data were also collected from sites that had burned in 1998 (five years prior to sampling, severity unknown: B-5), from sites that had been logged in 1993 (ten years prior to sampling: CC-10), and from undisturbed sites in the vicinity (undisturbed: UN-1, UN-5 and UN-10, respectively). For logistical reasons, sampling on sites disturbed less than one growing season prior to sampling was more thorough than that on sites disturbed five years and ten years prior to sampling. Sites disturbed less than one growing season prior to sampling were all in the IDF dk subzone, while those disturbed five and ten years prior to sampling occurred in both the IDF dk and the IDF xh subzones.

2.2.1 Sites disturbed less than one growing season prior to sampling

Sites disturbed by low severity fire less than one year prior to sampling (LB-1) were characterized by a living tree canopy dominated by *Pseudotsuga menziesii* (> 90% of trees alive and most of foliage green; ± scorching on bole) and a scorched (but not completely consumed) forest floor, approximately 1.0 cm deep (Figure 2.1a). Most of the available fuel on sites disturbed by high severity fire less than one year prior to sampling (SB-1) was completely consumed - remnant tree skeletons had no needles or small branches, and mineral soil was exposed over the entire site (Figure 2.1b). Although fire is heterogeneous at a variety of spatial scales, sites were required to be relatively uniform in terms of disturbance to the soil over an area of at least 50 m x 50 m. In the logged areas (CC-1), harvesting took place during the winter of 2003-2004 (approximately eight months prior to sampling) and harvested areas were at least 1.5 ha in size (Figure 2.1c). Following harvesting, the ground on all logged sites was mechanically disturbed to expose mineral soil either in pits approximately 0.5 m x 0.5 m x 0.5 m and 5 m apart, or in trenches approximately 0.5 m deep and 4-5 m apart. Sites in the vicinity that were not disturbed by fire or logging at this time (UN-1) were also sampled (Figure 2.1d). Although these sites are referred to as 'undisturbed', it is likely that non-stand-replacing disturbances such as wind-throw and livestock grazing had occurred on these sites (and the disturbed sites) throughout stand development. The largest tree on all undisturbed sites and most burned sites was cored to estimate the time since the last stand-replacing disturbance. The results indicated that all stands were more than 100 years old, and four stands were more than 200 years old; logged sites were assumed to be of the same age range. The forest floor on undisturbed sites was approximately 3.0 cm deep.

Four replicate sites for each of the four disturbance classes were sampled. One block of sites (containing one undisturbed site, one lightly burned site, one severely burned site, and one logged site, all in relatively close spatial proximity) was located in the Venables fire area near

Figure 2.1. Photos of (a) a site disturbed by low severity fire less than one year prior to sampling, (b) a site disturbed by high severity fire less than one year prior to sampling, (c) a site disturbed by logging less than one year prior to sampling, and (d) a mature Douglas-fir stand not recently disturbed.

a)

b)

c)

d)

Ashcroft, BC. The other three blocks were in the McClure fire area near Barriere, BC - one block (Oliver) was located on the east side of the Thompson River, and the other two blocks (Leonie and Jamieson) were towards the northern and southern boundaries of this fire on the west side of the Thompson River (Figure 2.2; Table 2.1).

Figure 2.2. Locations of study sites within the Kamloops Forest Region, and the extent of the IDF forest zone in British Columbia (inset). Sites disturbed one year prior to sampling are circumscribed by ellipses (Ashcroft, Jamieson, Leonie, and Oliver); each ellipse contains one site each of: UN-1, LB-1, SB-1, CC-1. Five-year-old burned sites and associated undisturbed sites were located at Greenstone Mountain (six sites in total - two at each point on the map), and ten-year-old logged sites were located at the Opax Mountain Silviculture Research Study Area (twelve sites in total - six at each point on the map).
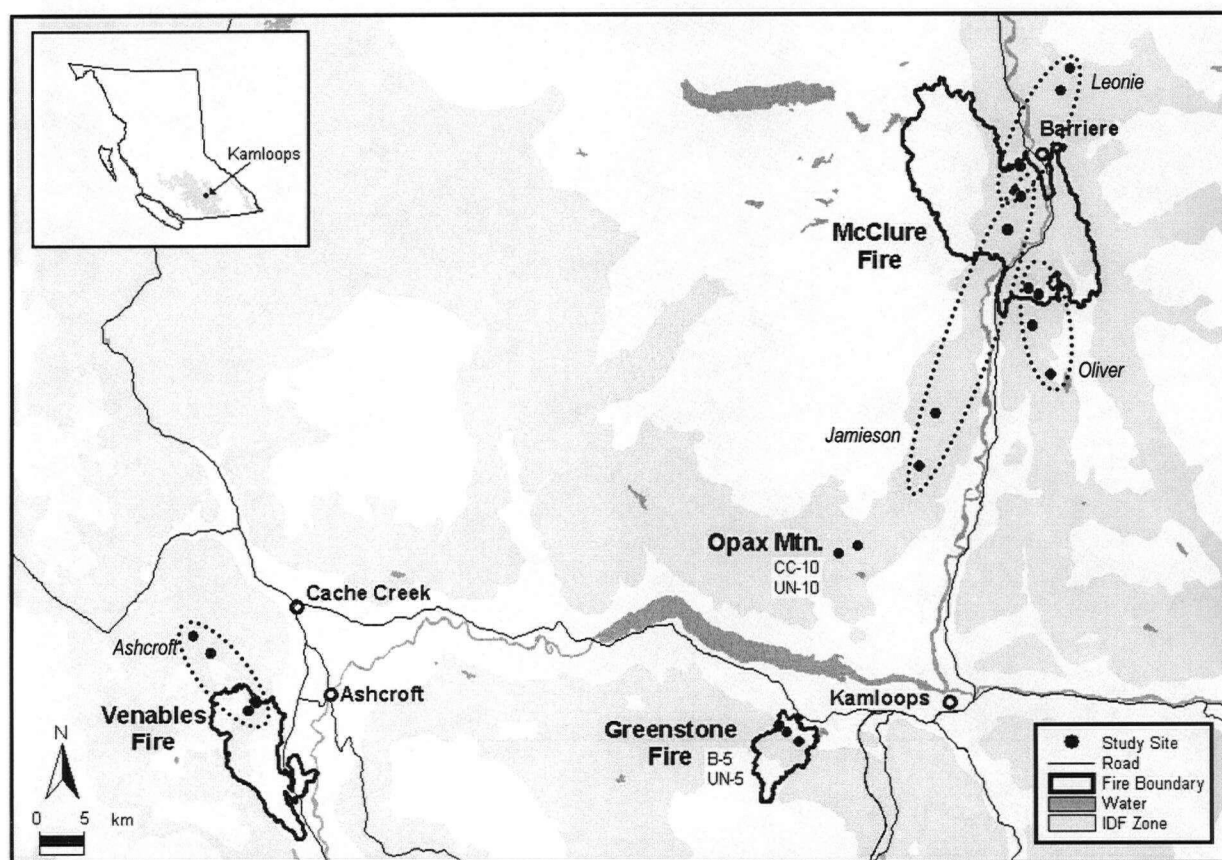
Within each site, sample collection locations were set up 10 m in each cardinal direction from a point in the centre of a relatively uniformly disturbed/undisturbed area. If the area 10 m from centre was deemed inappropriate, the first suitable location along the same trajectory was used, and the actual distance from the centre was noted. At each sampling location, four vegetation and five seed bank quadrats (three samples collected from each seed bank quadrat) were oriented in a grid pattern (Figure 2.3). In total on each site, sixteen 50 cm x 50 cm vegetation quadrats (four quadrats per grid) were sampled, and 60 soil samples (fifteen samples per grid) were collected to

Table 2.1. Characteristics of sites disturbed less than one year prior to sampling. UN-1: undisturbed, LB-1: lightly burned, SB-1: severely burned, and CC-1: logged.

Block	Disturbance	UTM co-ord.	Subzone	Aspect	Slope
Ashcroft	UN-1	10 U 0608866 5625401	IDF dk	South	45%
	LB-1	10 U 0613097 5619837	IDF dk	East	44%
	SB-1	10 U 0613066 5619530	IDF dk	East	48%
	CC-1	10 U 0607066 5627324	IDF dk	South	10%
Oliver	UN-1	10 U 0698742 5656200	IDF dk	North-West	26%
	LB-1	10 U 0698608 5659757	IDF dk	West	22%
	SB-1	10 U 0699392 5658983	IDF dk	North-East	20%
	CC-1	10 U 0700456 5650955	IDF dk	East	24%
Leonie	UN-1	10 U 0702872 5681027	IDF dk	South	20%
	LB-1	10 U 0697578 5670465	IDF dk	East	11%
	SB-1	10 U 0697509 5670563	IDF dk	East	12%
	CC-1	10 U 0703950 5683403	IDF dk	East	17%
Jamieson	UN-1	10 U 0685907 5641831	IDF dk	East	20%
	LB-1	10 U 0698174 5673150	IDF dk	East	35%
	SB-1	10 U 0696463 5666445	IDF dk	East	50%
	CC-1	10 U 0687907 5647354	IDF dk	East	5%

Figure 2.3. Spatial orientation of seed bank and vegetation plots. Three soil samples were taken from each "Seed Bank" plot (indicated with 'x'), and the vegetation was sampled in each 50 cm x 50 cm "Veg" plot. This resulted in a total of 15 seed bank samples and 4 vegetation plots per grid.
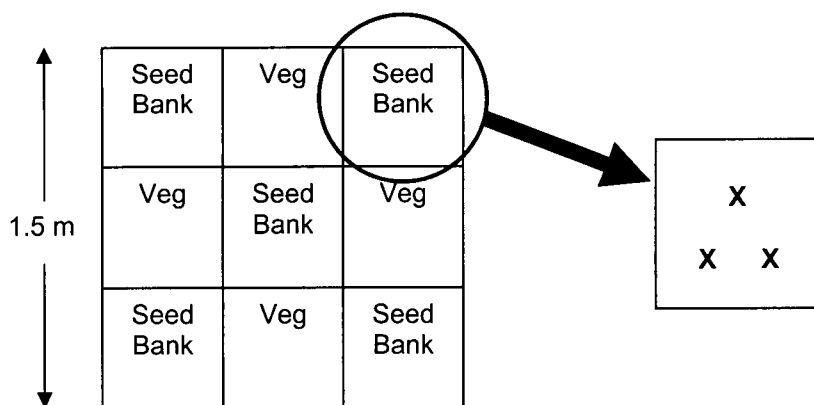
quantify the seed bank. Data from 64 vegetation quadrats and 240 soil samples were used to describe the vegetation and seed bank communities in each disturbance class (LB-1, SB-1, CC-1, and UN-1), thus data from a total of 256 vegetation quadrats and 960 seed bank samples were collected to evaluate vegetation and seed bank responses during the first year following disturbance.

Soil seed bank samples were collected between May 11 and May 21, 2004 following a natural *in situ* winter stratification period known to break dormancy in the seeds of many species (Baskin and Baskin 1998). At each seed bank sampling location (indicated with 'x' in Figure 2.3), eight 2 cm diameter soil cores were pooled to form one sample (total surface area = 25 cm^2). Cores

did not exceed a depth of 12 cm because the majority of the soil seed bank is concentrated at the top of the soil profile (McGee and Feller 1993; Warr et al. 1993). If a rock, root, or other obstruction was encountered above a depth of 12 cm, the obstruction was not moved, thus many cores did not penetrate 12 cm into the soil profile. To allow for comparisons among samples of different size, soil volumes were measured prior to set-up in the greenhouse. Any seeds that had already germinated at the sampling location were noted prior to soil removal, as they constituted part of the current year's seed bank.

Vegetation quadrats were sampled later in the growing season (June 25-July 4, 2004). Each 50 cm x 50 cm quadrat was subdivided into 25 10 cm x 10 cm subplots, and species presence was recorded in each subplot. Plants with prostrate growth forms (e.g. *Arctostaphylos uva-ursi*, *Linnaea borealis*, and *Paxistima myrsinites*) were recorded only in the subplots in which they were rooted. Root versus seed origin of the plants establishing on disturbed sites was determined by examination of the root system of representatives of each species. Species frequencies were calculated as:

(number of occupied 10 cm x 10 cm subplots) / (total number of subplots) x 100%.

2.2.2 Sites disturbed 5 and 10 years prior to sampling

Six 1.6 ha patch cuts harvested in 1993 and six undisturbed sites were sampled at the Opax Mountain Silviculture Research study area (Klenner and Vyse 1998) (Figure 2.2). Three sites that burned in 1998 and three unburned sites were also sampled at Greenstone Mountain (Figure 2.2). Fire severity on the burned sites was variable, and assignment into burn classes based on amount of forest floor consumed was not possible five years after disturbance.

Soil samples for the seed bank study were collected from these sites in October of 2003. At each site, three sampling locations with contrasting soil moisture and associated vegetation were selected (i.e. the perceived wettest and driest locations within the site based on topography and indicator plant species, as well as a location with a moderate moisture regime). At each sampling location, three 10 cm x 10 cm x 10 cm soil samples were taken from a 1 m^2 area. Soil samples were stored at temperatures between 0 and -2°C (soil temperature beneath a snow pack in the IDF; McLean 1967) from the time of collection until early January 2004 to stratify the seeds in the seed bank (Baskin and Baskin 1998).

Vegetation sampling at the sites disturbed five and ten years prior to sampling was conducted in July of 2004. Local frequency data were collected using a single 50 cm x 50 cm quadrat subdivided into 25 10 cm x 10 cm subplots at each seed bank sampling location, for a total of three vegetation quadrats per site.

2.3 Greenhouse procedure

The species composition and density of seeds germinating from the seed bank were determined using the seedling emergence method with the improvements suggested by Ter Heerdt et al. (1996). Specifically, each soil sample was wet-sieved to remove plant and rock material larger than the largest expected seed (4.0 mm sieve), and fine particulate matter smaller than the smallest expected seed (0.15 mm sieve). The soil samples were then spread in 0.5 cm thick layers over sterilized potting soil in 10 cm x 10 cm pots. Samples were exposed to a 16-h day-length regime (supplemented by artificial lighting when natural day lengths were less than 16 hours), and seedlings were identified, enumerated, and removed as they emerged, or else transplanted and grown until identification was possible. Upon cessation of germination, soil samples were placed in cold storage at 0°C to -2°C (McLean 1967) for 8 weeks then returned to the greenhouse to stimulate further germination. Samples were monitored in the greenhouse for a total of 18 weeks: 9 weeks + 8 weeks cold storage + 9 weeks for samples from sites disturbed one year prior to sampling; 12 weeks + 8 weeks cold storage + 6 weeks for samples from sites disturbed five and ten years prior to sampling. Greenhouse incubation periods differed, but longer germination periods were not associated with higher seed estimates because most germination occurred during the first few weeks of a given germination period. Although it is unlikely that all seeds germinated during the greenhouse incubation periods, for simplicity, those seeds and species that did germinate will hereafter be referred to as the seeds and species in the seed bank. The germination studies were carried out at greenhouse facilities at the University College of the Cariboo (now called Thompson Rivers University) in Kamloops, BC, and at the University of British Columbia in Vancouver, BC.

2.4 Statistical analysis
2.4.1. Univariate methods

Frequency distributions indicated that the data were positively skewed, so non-parametric statistical tests, which make no assumptions of normality, were used to analyze univariate measures of numbers of seeds and species in the seed bank, as well as frequencies of establishing vegetation of root and seed origin. Overall differences among disturbance types were assessed using Kruskal-Wallis tests. When Kruskal-Wallis tests returned significant p-values (p < 0.05), pair-wise comparisons were made using Mann-Whitney U-tests. All univariate tests were performed using SYSTAT statistical software (version 10; Anon. 2000).

2.4.2. Multivariate methods

Multi-Response Permutation Procedures (MRPP) was used to compare the species composition (a combined measure of species presence and relative frequency) of different groups (e.g. lightly burned vs. severely burned vs. logged vs. undisturbed; vegetation vs. seed bank).

Unlike multivariate analysis of variance (MANOVA), MRPP does not assume multivariate normality or homogeneity of variances. Because the data used here were not normally distributed, MRPP (using the Sørensen distance measure) was used (McCune et al. 2002). When two groups were found to differ using MRPP, Dufrêne and Legendre's (1997) Indicator Species Analysis (ISA) was used to determine which species were both faithful (i.e. always present in a group) and exclusive (i.e. never present in other groups) to which groups, and thus associated with the overall group differences (McCune et al. 2002). Nonmetric Multidimensional Scaling (NMS), again using the Sørensen distance measure, was used to generate ordinations that helped to further elucidate and visualize the relationships found with MRPP. Each ordination began with a random starting configuration, and forty 'runs' were made with real data, then 50 'runs' were made with randomized data to determine whether the axes extracted by NMS were stronger than those expected by chance. Final stress and instability values were noted. All multivariate analyses were performed using PC-ORD statistical software (version 4; McCune and Mefford 1999).

2.4.3 Disturbance effects on seed banks and vegetation: analysis for Chapter 3

The numbers of species and seeds in soil seed bank samples were compared using Kruskal-Wallis tests, and pair-wise comparisons between treatments were made using Mann-Whitney U-tests. Frequencies of vegetation of root and seed origin that established following disturbance were calculated, and comparisons of these frequencies were made using Kruskal-Wallis tests and Mann-Whitney U-tests. For this analysis, sites were used as sample units, thus there were four replicate sites per disturbance class in areas disturbed less than one year prior to sampling, three replicate sites in areas burned five years prior to sampling (and three corresponding undisturbed sites), and six replicate sites in areas logged ten years prior to sampling (and six corresponding undisturbed sites).

The number of seeds of each species in each seed bank sample was converted to a site-level frequency:

(number of 50 cm x 50 cm quadrats with ≥ 1 seed) / (number of quadrats on the site)

for comparison with site-level vegetation frequencies. MRPP was used to test for differences in species composition between disturbance classes within and between seed bank and vegetation communities. When two groups were found to be different using MRPP, Indicator Species Analysis was used to determine which species were associated with the difference. NMS with a Sørensen distance measure was used to generate ordinations showing the relationships among vegetation and seed bank communities following different types of disturbance.

2.4.4 Spatial heterogeneity in seed banks and vegetation: analysis for Chapter 4

To examine among-site differences in the species composition of both seed bank and vegetation communities, the data were grouped so that four grids represented each site. Within each disturbance class, differences in species composition between each pair of sites were assessed using MRPP. A total of six pair-wise comparisons was possible among the four sites per disturbance class. To summarize the comparisons, a heterogeneity index (the number of significantly different pair-wise comparisons divided by the total number of pair-wise comparisons) was calculated for each disturbance class.

To assess within-site differences in species composition, the data were again grouped so that five seed bank quadrats or four vegetation quadrats represented each grid. Comparisons of all possible pairs of grids within each site were made using MRPP; a total of six pair-wise comparisons was possible within each site, giving a total of twenty-four possible pairs within the four sites of each disturbance class. In some cases on the more severely disturbed sites, seed bank samples did not contain any seeds and/or vegetation quadrats were empty; when this occurred, the number of pair-wise comparisons was less than the maximum. A heterogeneity index, similar to that for the among-site comparisons, was calculated for within-site comparisons. Seed bank communities were compared to vegetation communities at both spatial scales.

Species-area curves were generated to evaluate how many seed bank samples were required to account for the majority of present species and thus address how seed bank heterogeneity affects seed bank sampling methods. In addition, actual numbers of species sampled were compared to jackknife estimates of true species richness (calculated using information on the number of species observed, the number of species that occurred in only one sample unit, and the number of sample units) within each disturbance class. An overall estimate of sampling efficiency was calculated as the ratio of observed to estimated numbers of species.

3. DISTURBANCE, SEED BANK, AND ESTABLISHING VEGETATION COMMUNITIES

3.1 Overview

The soil seed bank and vegetation establishing on sites disturbed by low severity fire, high severity fire, and logging in Interior Douglas-fir forests were examined on sites disturbed the summer prior to sampling, and on sites burned five years prior to sampling or logged ten years prior to sampling. The objectives of this chapter are to:

(i) determine the number of seeds, the number of species, and the species composition of soil seed banks disturbed by fire or logging less than one year prior to sampling,

(ii) compare the species composition of this *potential* seed-derived community to that of the *actual* plant communities that established in the field during the first post-disturbance growing season, and

(iii) compare seed bank and vegetation communities on sites disturbed five and ten years prior to sampling by fire and logging (respecitvely) to those on neighbouring undisturbed sites.

3.2 Results

3.2.1 General characteristics of seed banks and vegetation communities

Seeds from a total of 74 taxa germinated from soil samples during greenhouse germination trials (Table 3.1). Thirty (40%) of these taxa did not occur in the vegetation that was sampled in the immediate vicinity of seed bank sample origin (all sites and disturbance types combined). The most abundant taxa in the seed bank and the percentage of samples in which they were present were *Epilobium ciliatum* (38%), *Epilobium angustifolium* (28%), *Cirsium vulgare* (16%), *Poa* sp. (16%), and *Carex* spp. (9%).

Eighty-seven taxa were recorded in vegetation communities. The most frequent taxa in the vegetation and the percentage of quadrats in which they occurred were *Calamagrostis rubescens* (64%), *Arnica cordifolia* (32%), *Epilobium angustifolium* (29%), and *Spiraea betulifolia* (28%). Of the 117 taxa encountered in this study (seed bank and vegetation communities combined), seventeen (15%) were not native to North America. Eleven of these exotic species were restricted to the seed bank, while the remainder occurred in both the seed bank and the vegetation (Table 3.1).

3.2.2 Disturbance effects on the soil seed bank

The soil seed banks on sites disturbed by fire or logging less than one year prior to sampling contained both fewer seeds and fewer species than the seed banks on neighbouring undisturbed sites (Figure 3.1). A median density of 470 seeds/m^2 was recorded on undisturbed sites, whereas median densities of 80-174 seeds/m^2 were recorded on the disturbed sites (Figure 3.1a). Similarly, the median species richness on undisturbed sites was 17 species compared to medians of 5-8 species on the disturbed sites (Figure 3.1b).

Table 3.1. Percentage of 50 cm x 50 cm quadrats in which each taxon occurred in the seed bank and vegetation communities that established following disturbance by logging one year and ten years prior to sampling (CC-1, CC-10), by fire (low and high severity) one and five years prior to sampling (LB-1, SB-1, B-5), and on undisturbed sites in the vicinity of the disturbed sites (UN-1, UN-5, UN-10). Species not native to North America are indicated with *.

Species	Seed Bank								Vegetation							
	UN-1	LB-1	SB-1	CC-1	UN-5	B-5	UN-10	CC-10	UN-1	LB-1	SB-1	CC-1	UN-5	B-5	UN-10	CC-10
Achillea millefolium							14	8	3	9					12	39
Agropyron sp.										3						
Agropyron spicatum									3	8				11	6	
Allium cernuum								3	16	28	3		22		18	17
Alnus incana					44			6								
Alnus viridis								22								
Amelanchier alnifolia									5			3				
Anethum graveolens*				2												
Antennaria sp.	10	3	2	2		7	25	25		13		2	11	33	41	28
Aquilegia formosa	2											2				
Arabis holboellii	12	7			7		3	11	8	11					12	22
Aralia nudicaulis									5			13				
Arctostaphylos uva-ursi									13	2	5	3			18	33
Arnica cordifolia							12		33	27	25	20	11	11	76	50
Aster conspicuus									6	2		2				
Aster foliaceous									2							
Aster sp.		3	2				6		2	2		2		44	24	28
Astragalus miser		.							13	2	3				29	17
Balsamorhiza sagittata											3					
Betula papyrifera	48	3		3						3	5					
Brassicaceae					4	11										
Bromus sp.												2				
Calamagrostis rubescens					4	4	10	34	73	48	42	53	67	56	76	94
Campanula rotundifolia					4			6								6
Carex sp.	15	2	7	5	41		48	14	20	17	27	9	11	33	24	50
Caryophyllaceae														22		
Castilleja sp.																17
Cerastium fontanum*	5			2	7	4	18	28		2						
Chenopodium album*								6								
Chimaphila umbellata									25			11				
Cirsium vulgare*		8		8	56	44	6	6		4	2	2			6	
Clematis occidentalis									2							
Clintonia uniflora									8			6				
Collinsia parviflora	8	5			11		15	6	8	22	9		11		12	
Collomia linearis					7		6	7							12	17
Conyza canadensis*	2															
Cornus canadensis									16			17			6	
Cornus stolonifera									3	11		3				
Descurainia sophia*					7											
Disporum hookeri									6							
Elymus glaucus															18	6
Elymus repens*							24	6								

Species	Seed Bank								Vegetation							
	UN-1	LB-1	SB-1	CC-1	UN-5	B-5	UN-10	CC-10	UN-1	LB-1	SB-1	CC-1	UN-5	B-5	UN-10	CC-10
Epilobium angustifolium	8	13	17	2	15	52	66	54	3	77	47	30		44	6	22
Epilobium ciliatum	17	7	5	5	44	78	72	78		9	2	2				
Epilobium sp.					11	6	7									
Equisetum sylvaticum																6
Erigeron flagellaris					7	4			2	2						
Festuca ovina							6	11								
Festuca sp.												2				
*Filago arvensis**	3															
Fragaria vesca	10			3	4		2	17	14	2						
Fragaria virginiana	2						2		6	3					47	78
Galium boreale									2			2				
Galium triflorum	15						6		11						12	
Geum macrophyllum					4		6	6								6
Goodyera oblongifolia									17	2			11	11	24	6
Hieracium albiflorum									5				11	11	24	44
Hieracium umbellatum	2															
Juncus bufonius	3												11			
*Lactuca serriola**					4	4							11	22		6
Lathyrus nevadensis									14		2					
Lathyrus ochroleucus	2								3							
Lathyrus sp.															24	17
Linnaea borealis				2					52	6		28			12	11
Mahonia aquifolium									16	2		6			18	11
*Medicago lupulina**					19											
*Medicago sativa**												13				
Mitella nuda		5			11	4										
Orthilia secunda									19			8			12	11
Oryzopsis pungens								2								
Osmorhiza chilensis									13			8		11	35	
Paxistima myrsinites	8								34	5	6	28			12	22
Pedicularis bracteosa									2							
Picea sp.	2						12	6		2						
Pinus contorta									11	5	16	20				
Plantago major	2			2	7	4	6									
Poa compressa						56		11								
Poa secunda								6								
Poa sp.	40	8	2		44	33	12	36	8							
*Polygonum convolvulus**								6								
Polygonum douglasii						3		6	6	6					6	11
Populus tremuloides	12	20	18	2						45	20	5		11	6	6
Potentilla arguta					11			6								
Potentilla diversifolia	2															
Potentilla norvegica							18	17								
Pseudotsuga menziesii		3				2	12	6	11	48	8	5	22	56	12	
Ranunculus sp.									2			2				
Ranunculus uncinatus							6									
Ribes lacustre	3															
Rosa acicularis										16	2	8		11	18	17
Rosa gymnocarpa												3				

Species	Seed Bank								Vegetation							
	UN-1	LB-1	SB-1	CC-1	UN-5	B-5	UN-10	CC-10	UN-1	LB-1	SB-1	CC-1	UN-5	B-5	UN-10	CC-10
Rosa nutkana												3				
Rosa woodsii									14			3				
Rubus idaeus	5			2												6
Rubus parviflorus	10								6						6	
Rubus sp.	2								17	8						
*Sagina apetala**				2												
Salix spp.	3	2	5	2								2		22		
Sedum lanceolatum	12			3					6	2						
Shepherdia canadensis		2										3				
Smilacina racemosa									8			2			12	
*Sonchus arvensis**	2						6									
Sorbus sp.															12	
Spiraea betulifolia			5	17		11	2	17	33	45	17	28		11	41	50
Symphoricarpos albus									9	5	11	2			18	22
*Taraxacum officinale**	2				11	4	18		2	2				33	24	56
Thalictrum occidentale									5						18	6
Tragopogon dubius										2	2		11			
Typha latifolia	5	5		2												
Vaccinium sp.									2		2	16				17
*Verbascum thapsus**	3				11	7		41								6
Veronica beccabunga					4											
*Veronica serpyllifolia**								17								
Vicia americana		2					6	6			2				18	22
Viola adunca									2							
Viola canadensis					11	12									24	17
Viola sp.	10															
Unknown dicot	52	32	13	8	22		12	29	16	42	8	18	11	33	18	22
Unknown grass														11	24	28
Unknown monocot	23	8	2	10	4	4	3	5	6	13		8				
Unknown sprout										8					12	28

Figure 3.1. Box plots showing a) the number of seeds/m^2 soil and b) the total number of species in the seed bank on sites disturbed less than one year prior to sampling (CC-1 = logged, LB-1 = lightly burned, SB-1 = severely burned) and on undisturbed sites in the vicinity (UN-1). Medians are indicated with horizontal lines inside boxes; boxes with the same letter are not significantly different (p > 0.05).
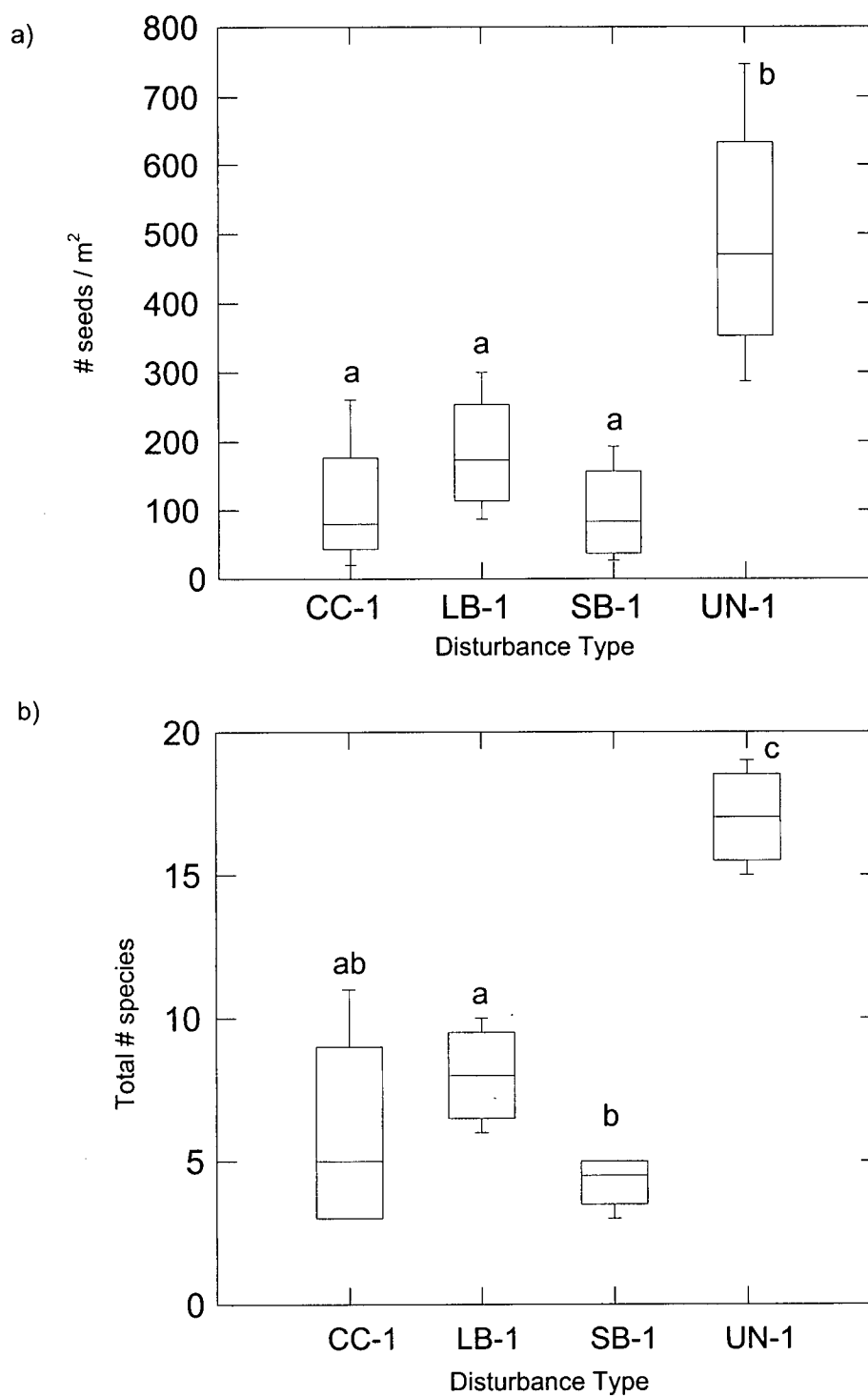
The species composition of seed banks on sites disturbed by severe fire and logging differed significantly from that on undisturbed sites (MRPP: p = 0.01 and p = 0.04, respectively). In contrast, the species composition of seed banks on lightly burned and undisturbed sites did not differ significantly (MRPP: p = 0.07). There were no indicator species associated with the differences in species composition between logged, severely burned, and undisturbed seed banks because the many species in common among different sites prevented the 'exclusive' criterion of ISA from being met. Nevertheless, *Galium triflorum*, *Rubus parviflorus*, and *Viola* sp. occurred in > 10% of undisturbed seed bank samples, but were absent from the seed banks on disturbed sites (Table 3.1). There were no significant differences in seed bank species composition among sites disturbed by light burning, severe burning, or logging less than one year prior to sampling (MRPP: p > 0.05 for all pairs).

The species composition of seed banks on sites disturbed by fire five years prior to sampling and on sites disturbed by logging ten years prior to sampling did not differ from those on corresponding undisturbed sites (MRPP: p > 0.05); however, differences in abundance between disturbed and undisturbed sites were observed for some species. For example, *Epilobium angustifolium* was more than three times more abundant in the seed banks on five-year-old burned sites than on undisturbed sites in the vicinity, and two exotic species (*Veronica serpyllifolia* and *Verbascum thapsus*) that were absent from the seed banks on undisturbed sites were found in 17% and 41% of seed bank samples on ten-year-old logged sites, respectively (Table 3.1).

3.2.3 Seed bank vs. vegetation

The species composition of the seed bank differed significantly from that of the vegetation on undisturbed sites (MRPP: p < 0.001), on sites disturbed by low severity fire (MRPP: p = 0.01) or logging (MRPP: p = 0.01) less than one year prior to sampling, and on sites disturbed by fire five years prior to sampling (MRPP: p = 0.02) or logging ten years prior to sampling (MRPP: p < 0.001) (Figure 3.2). High frequencies of *Epilobium angustifolium*, *Epilobium ciliatum*, *Carex* sp., and *Poa* sp. in the seed bank, and *Arnica cordifolia*, *Goodyera oblongifolia*, *Linnaea borealis*, and *Rosa* spp. in the vegetation were associated with the differences (ISA: p < 0.05 for all species listed). The species composition of the seed bank and that of the vegetation did not differ significantly on sites disturbed by high severity fire less than one year prior to sampling (MRPP: p = 0.1) (Figure 3.2). For the NMS ordination of seed bank and establishing vegetation communities (Figure 3.2), the three-dimensional solution accounted for 70% of the variation in the data (53% for the two axes shown), but high stress (21.9) and instability (0.026) suggest that the ordination should be interpreted with caution. Axis 1 separated seed bank from vegetation communities, while Axis 3 separated five- and ten-year-old disturbed and corresponding undisturbed sites (which occurred in

both IDF dk and IDF xh subzones) from sites disturbed less than one year prior to sampling (which were all in the IDF dk subzone) (Figure 3.2).

Figure 3.2. NMS ordination of seed bank (sb) and vegetation (veg) communities on sites disturbed by logging (CC-1), low severity fire (LB-1), and high severity fire (SB-1) less than one growing season prior to sampling, on sites disturbed by fire five years prior to sampling (B-5), on sites disturbed by logging ten years prior to sampling (CC-10), as well as on undisturbed sites in the vicinity (UN-1, UN-5, and UN-10 pooled: UN).
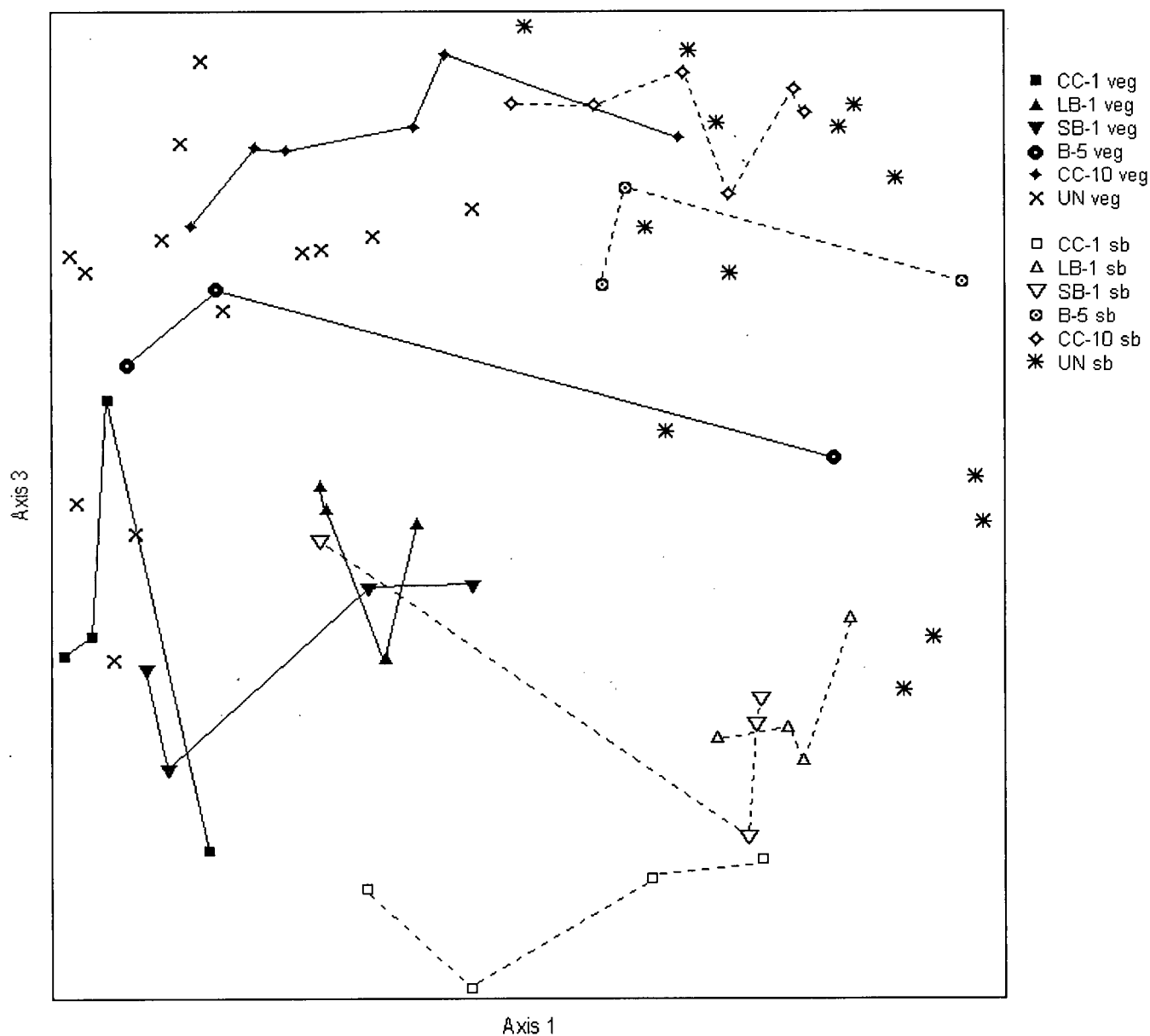
3.2.4 Seed and root contributions to the establishing vegetation community

The frequency of plants germinating from seed on sites disturbed less than one year prior to sampling differed such that lightly burned > severely burned > logged, but neither logged sites nor severely burned sites differed from undisturbed sites (Figure 3.3). Further, the seed-derived plant frequencies on lightly burned and severely burned sites were more variable (indicated by longer boxes in Figure 3.3) than were those on logged sites. The species composition of seedling communities in the field did not differ from that of adjacent soil seed banks on sites disturbed by low or high severity fire (MRPP: $p = 0.05$ and $p = 0.5$, respectively). In contrast, the species composition of seed bank and field seedling communities differed significantly on logged sites (MRPP: $p = 0.007$) because of the infrequency of germinants in the field. The remainder of the vegetation on disturbed sites arose from persistent root structures. No significant differences in frequency of root-derived plants were detected among any of the one year disturbed sites. Perennial plants arising from established root systems were significantly more frequent on undisturbed than disturbed sites (Figure 3.3).

3.2.5 Post-disturbance plant community composition

The species composition of the establishing vegetation communities on lightly burned and severely burned sites did not differ from each other (MRPP: $p = 0.2$), but the total frequency of vegetation was significantly higher on lightly burned sites (Figure 3.3). Species with consistently higher frequencies on lightly burned sites included *Allium cernuum*, *Cirsium vulgare*, *Collinsia parviflora*, *Epilobium ciliatum*, *Populus tremuloides*, *Pseudotsuga menziesii*, *Rosa acicularis*, and *Spiraea betulifolia* (Table 3.1). Total vegetation frequency did not differ between lightly burned and undisturbed, or between severely burned and undisturbed sites (Figure 3.3). The species composition of the vegetation that established during the first growing season following low severity and high severity fires was significantly different from that on neighbouring undisturbed sites (MRPP: $p = 0.01$ and $p = 0.01$, respectively). The differences between the burned and undisturbed sites were associated with a higher frequency of *Calamagrostis rubescens* on undisturbed sites, and higher frequencies of *Epilobium angustifolium* and *Pseudotsuga menziesii* seedlings on the burned sites (ISA: for all species listed $p < 0.05$). The vegetation on logged sites did not differ from that on undisturbed sites in terms of species composition (MRPP: $p = 0.09$), but total species frequency was significantly lower on the logged sites (Figure 3.3).

While overall species composition did not differ between five-year-old burned and neighbouring undisturbed sites, and ten-year-old logged and neighbouring undisturbed sites (MRPP: $p = 0.6$ and $p = 0.1$, respectively), some species (e.g. *Epilobium angustifolium*, *Fragaria virginiana*, and *Spiraea betulifolia*) were notably more frequent on disturbed than undisturbed sites (Table 3.1).

Figure 3.3. Box plots showing frequency of plants of seed origin, root origin, and total vegetation frequency (seed and root origin plants combined) on sites disturbed by logging (CC-1), low severity fire (LB-1), and high severity fire (SB-1) less than one year prior to sampling, and on undisturbed sites (UN-1) in the vicinity. Within each origin class (i.e. seed origin, root origin, total), boxes with the same letter are not significantly different (p > 0.05).
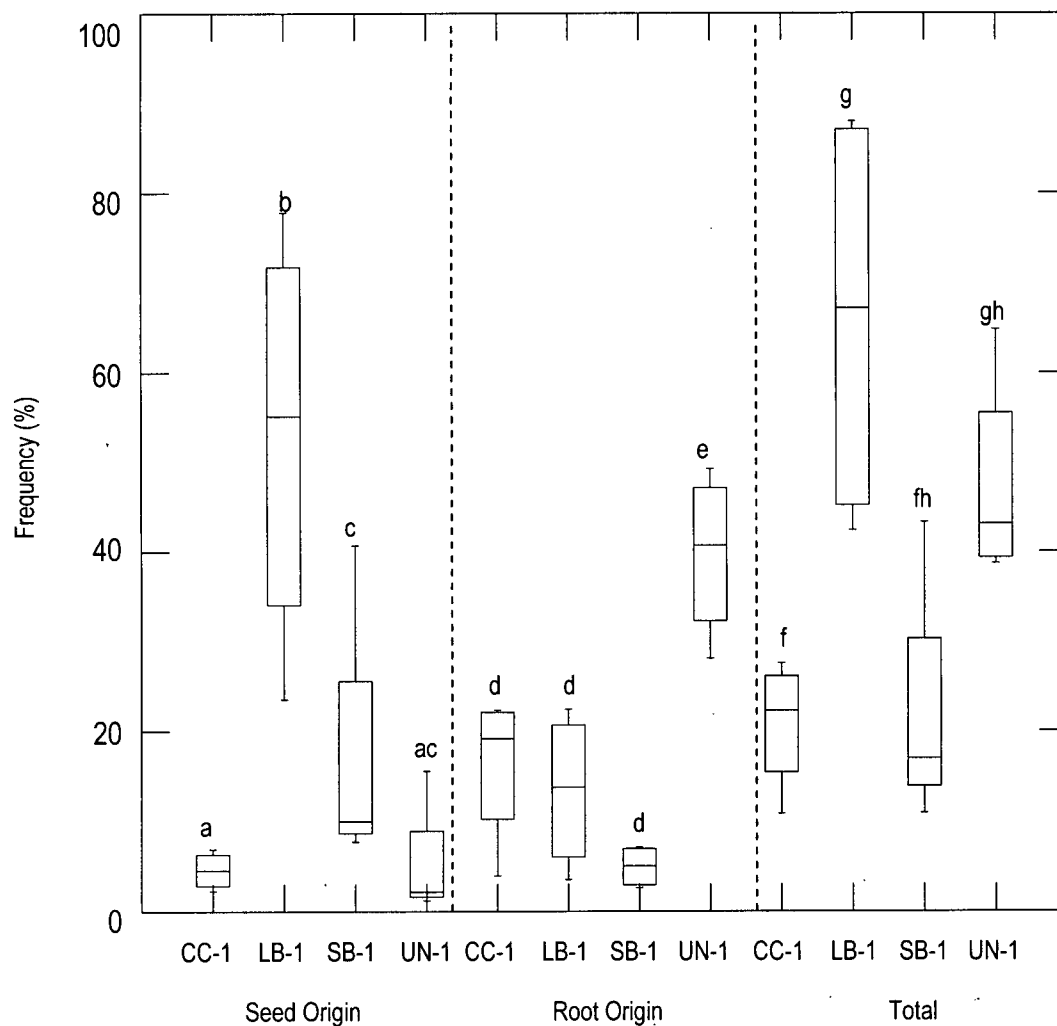
3.3 Discussion

3.3.1 Seed bank and vegetation response to disturbance

The observed lack of difference between lightly burned and severely burned sites in seed density and species composition of the seed bank, and in frequency of root-derived plants and overall species composition of establishing vegetation communities is likely associated with the minor difference in post-fire forest floor depth (< 1 cm) following the two severities of fire. Unlike boreal forest systems where forest floors can exceed 20 or 25 cm in depth (e.g. Dyrness and Norum 1983), the 3 cm thick forest floors on the undisturbed IDF sites sampled here did not have much

potential for differential responses to fire. Forest floor consumption was somewhat patchy on the lightly burned sites, but on severely burned sites, consumption of the forest floor and associated seed bank was uniform and complete. Despite the general lack of difference between lightly burned and severely burned sites in the variables mentioned above, more species were present in seed banks on lightly burned sites. It is possible that samples collected from less-disturbed areas on the unevenly scorched forest floors of lightly burned sites contained some of the species that were absent from the seed banks of severely burned sites, but that these species were not present in high enough numbers to influence overall seed bank species composition or seed density.

An important ecological difference between fire and logging disturbances is that mixing of upper soil horizons normally accompanies logging. As parts of the forest floor are buried and patches of mineral soil exposed, the usual stratification of propagules in the forest floor is lost, and contributions of stored structures to post-disturbance communities becomes more stochastic. Qi and Scarratt (1998) proposed that newly exposed mineral soil might contain long-buried seeds, and the parts of the seed bank that were concentrated in the upper soil horizons would be lost with forest floor burial. In spite of probable differences in disturbance to the forest floor, some of the post-disturbance trends observed on lightly burned and severely burned sites were also found on logged sites. Specifically, the numbers of seeds and species in soil seed banks, and the frequency of root-derived plants in the post-disturbance community did not differ between burned sites (both severities) and logged sites.

3.3.2 Post-disturbance seed arrivals

Although this study was not designed to discriminate between plants originating from seed stored *in situ* for the duration of the disturbance, and those originating from seed that arrived after disturbance, it is worth noting that some of the most abundant taxa in the seed bank and seed-derived vegetation communities on post-fire sites likely arrived during the first autumn and spring following disturbance. Specifically, *Epilobium angustifolium, Populus tremuloides, Pseudotsuga menziesii*, and *Salix* spp. were among the top five most abundant taxa in seed bank and establishing vegetation communities on burned sites, and seeds of these taxa are known to remain viable in the soil for one year or less (Granström 1987; US Forest Service 2005). In contrast, many of the species that necessarily arrive after disturbance either were entirely absent from logged sites (*Picea* sp., *Pinus contorta*), or were present in the seed bank but absent from the vegetation community on logged sites (*Betula papyrifera*), or were present in the vegetation on logged sites but in low numbers compared with presence in post-fire communities (*Populus tremuloides, Pseudotsuga menziesii*).

The abundance of seed that likely dispersed onto burned sites and the infrequent occurrence of these species in seed banks on logged sites could be attributed to: i) the relative uniformity with

which potential seed trees were removed from logged sites, ii) the relative distances of sampling locations from seed sources at the edges of burned and logged areas, iii) differences in the species available to function as seed sources following fire and logging, and iv) possible enhancement of seed dispersal during fire events. Seed deposition generally decreases in a negative exponential curve with increasing distance from the source plant (Chambers and MacMahon 1994), and many studies have shown a seed-limitation-induced decline in natural conifer regeneration with distance from edge of clearcut (e.g. Timoney and Peterson 1996; Hughes and Bechtel 1997). Although the extent of many of the areas disturbed by fire was larger than the size of the logged areas, fires are inherently variable in terms of severity. Often patches of forest (both large and small) escape burning and persist within the burned matrix to function as seed sources (Turner et al. 1994). Variable-retention logging practices also leave clusters of seed-trees, but none of the logged sites sampled was of this type. Local events such as dispersal from residual plants might have affected herbaceous plant distributions at smaller scales (Landenberger and McGraw 2004). In addition to issues of disturbance size, the convective air movements and vortices associated with fire might actually have enhanced seed dispersal over burned areas (Pisaric 2002).

3.3.3 Seed bank contributions to the post-disturbance vegetation community

Regardless of when they arrived, all of the seeds in the seed bank at any given moment comprise a pool of potential seed-origin individuals. Many authors have speculated that the seed bank could provide an important source of species during post-disturbance succession (e.g. Strickler and Edgerton 1976; Pratt et al. 1984), but few have compared the species in the seed pool to the species that actually germinate following disturbance (Beatty 1991; Yearsley 1993; Hyatt 1999; Lee 2004). While seed germination is often inhibited in mature, closed-canopy forests (Pratt et al. 1984), the seeds of many species are released from dormancy by the alterations to light and temperature regimes at the soil surface that accompany disturbance (Kramer and Johnson 1987). Only 32% of the seed bank species on undisturbed sites were present in the vegetation in the immediate vicinity of seed bank sample collection as seedlings or mature plants, but this increased to 63% on disturbed sites. This increase in agreement between seed bank and vegetation is likely associated with the changes to the seed environment that accompanied the disturbances.

Although the actual proportion of the seed bank detected in this study is not known, Ter Heerdt et al. (1996) reported that when their suggested modifications to the seedling emergence method were used, 80-100% of the seed bank germinated during greenhouse germination trials. In this study, the numbers of seeds and species found in the seed bank using the methods suggested by Ter Heerdt et al. (1996) did not differ significantly across disturbance types, but the frequency of seed-derived plants that germinated in the field differed in the order: lightly burned > severely burned > logged. The assemblage of species in the seed bank did not differ in composition from

that of germinants in the field on lightly burned and severely burned sites, but seed bank and seedling communities differed on logged sites. Both these differences in species composition and the observation that more species germinated in the greenhouse than in the field suggests that germination from the seed bank was inhibited or that seed predation or seed/seedling mortality were high under field conditions on logged sites.

Many of the species that were abundant in the seed bank on severely burned sites had dispersal and germination capabilities that allowed them to be successful in a burned environment (e.g. small, light seeds, and a preference for mineral soil as a germination substrate; Zasada et al. 1983). Because of such attributes, the potential seed-derived community was fully realized on severely burned sites. Root-derived plants were less frequent than seed-derived plants, and the overall composition of the vegetation that established post-severe-burn did not differ from that of the seed bank on these sites. On lightly burned sites, although species such as *Epilobium angustifolium* and *Pseudotsuga menziesii* established from seed and were important constituents of the post-light-burn vegetation community as they were in the post-severe-burn vegetation community, root-derived species such as *Arnica cordifolia*, *Calamagrostis rubescens*, and *Spiraea betulifolia* also sprouted vigorously and formed an important part of the post-light-burn community. The consequence of the success of these root-derived species was a weaker correspondence between the seed bank and the vegetation communities on lightly burned sites. The similar weak correspondence between seed bank and vegetation observed on the one-year-old logged sites was associated with low numbers of seed bank germinants in the field.

3.3.4 Seed bank and vegetation relationships five and ten years after disturbance

Five years after disturbance by fire and ten years after disturbance by logging, the major contributions of the seed bank to the post disturbance community seem to have been made. The proportion of seed bank species represented in the vegetation was 44% on the five-year-old burned sites, and it was 42% on ten-year-old logged sites. In comparison, 64% of seed bank species were represented in the vegetation on sites disturbed one year prior to sampling. The lack of difference between seed bank species assemblages on five-year-old burned sites and ten-year-old logged sites and those on their corresponding undisturbed sites suggests that seed dispersal processes have eliminated any differences that existed initially based on the comparison of the one-year-old disturbed and undisturbed sites. Similarly, vegetation communities have developed such that any initial differences in species composition that might have existed between burned or logged sites and corresponding undisturbed sites are no longer significant.

Egler (1954) argued that the majority of species that would eventually develop on a site following disturbance were present as either seeds or seedlings immediately following disturbance, and changes to the post-disturbance community were simply the result of changes in dominance of

different species groups over time. Even though overall differences in species composition between five-year-old burned sites, ten-year-old logged sites and corresponding undisturbed sites were not significant, some disturbance-tolerant, early-successional species occurred with higher frequency on the disturbed sites (e.g. *Epilobium angustifolium, Taraxacum officinale,* and *Verbascum thapsus*). A number of shade-tolerant, later-successional species occurred on both logged and undisturbed sites, but with higher frequency on undisturbed sites (e.g. *Goodyera oblongifolia, Thalictrum occidentale,* and *Viola canadensis*). Barring further disturbance, it is expected that the disturbance-tolerant species will decline in frequency and the shade-tolerant species will increase in frequency as canopy closure progresses.

3.3.5 Management implications

The possibility of improved conditions for germination and spread of exotic species following disturbance by fire or logging is an important forest management consideration in the IDF vegetation zone. Seed banks can function as reservoirs that hold species on a site between disturbances (e.g. Harper 1977). Concern arises when growing conditions suitable for undesirable, weedy species contained in the seed bank are promoted by disturbance (Warr et al. 1993; Qi and Scarratt 1998). In this study, sixteen exotic species were found in soil seed banks. Field germination conditions prevented most of these species from establishing in the field - only six exotic species were found in vegetation communities. Three of these species (*Cirsium vulgare, Lactuca serriola,* and *Taraxacum officinale*) were found in both disturbed and undisturbed vegetation communities, which shows that some weedy exotic species (particularly those with light, wind-dispersed seeds) are able to both disperse and recruit into mature, intact vegetation communities.

Although all potentially important differences between fire and logging were not quantified in this study (e.g. differences in the amount of woody biomass left after these types of disturbance), for the parameters considered here, the plant communities that established during the first post-disturbance growing season on logged sites had more in common with those on severely burned sites than with those on lightly burned sites. Forest management practices that incorporate more low severity disturbances to balance low and high severity disturbances across the landscape might therefore be required to better mimic the mixed severity fire regime that characterizes IDF forests. Prescribed low severity burning in intact forests, and/or logging practices that more closely resemble low severity fire could be considered to meet this objective. Because of limitations in long distance seed dispersal into large clearings, plant community development on logged sites might be restricted to local expansion of species already present via both local seed production and dispersal, and lateral vegetative spread (Egler 1954; Qi and Scarratt 1998). The infrequency of conifer seeds on logged sites immediately following disturbance suggests that conifer regeneration

will be dependent on the success of planted seedlings. Following fire, natural regeneration of conifer species was scattered but significantly more frequent than that on logged sites. The lack of overall difference between plant communities on five-year-old burned sites, ten-year-old logged sites, and corresponding undisturbed sites suggests that vegetation recovery might occur rapidly; however, the success of planted seedlings (Huggard et al. 2005), and changes to the vegetation over longer time scales also need to be considered to fully understand long-term post-disturbance vegetation dynamics.

4. SPATIAL HETEROGENEITY IN SEED BANK AND VEGETATION COMMUNITIES

4.1 Overview

In Chapter 3, seed bank and vegetation communities were described following disturbance by fire and logging in Interior Douglas-fir forests. While both similarities and differences in seed bank and vegetation species composition were noted among disturbance types, heterogeneity within disturbance types was not examined. In this chapter, the data from one-year-old disturbed and corresponding undisturbed sites are re-examined to focus on differences in species composition of soil seed banks and vegetation communities within each disturbance class both *among* sites (using the four grids per site as replicates) and *within* sites (using the five seed bank or four vegetation quadrats per grid as replicates). The objectives of this chapter are to:

(i) determine the extent to which the species composition of soil seed banks on undisturbed sites varied at coarse (among-site) and fine (within-site) spatial scales,

(ii) describe how among- and within-site heterogeneity in seed bank and vegetation species composition is affected by disturbance, and

(iii) determine the effectiveness of the sampling design used in this study for estimating the total number of species in soil seed banks subject to different types of disturbance.

4.2 Results

4.2.1 Heterogeneity in soil seed banks

Seed bank species composition varied greatly among undisturbed sites, while within sites, the heterogeneity of undisturbed seed banks was among the lowest observed (Figure 4.1a). The heterogeneous distribution of *Betula papyrifera* seeds was partially responsible for differences at both spatial scales, and the presence of *Viola* sp. on one site added to the among-site differences (ISA: $p < 0.05$; Table 4.1). Seed bank communities on disturbed sites were less variable than were those on undisturbed sites, although approximately half of the pair-wise comparisons indicated that communities were different (Figure 4.1a). Differences in species composition among burned sites were associated with different numbers of *Populus tremuloides* seeds on different sites (ISA: $p < 0.05$; Table 4.1). The scattering of non-zero entries in Table 4.1 suggests an overall trend of patchiness in the soil seed banks sampled here, regardless of disturbance type.

The species composition of soil seed bank sample units within lightly burned sites was not particularly variable, while that within logged sites and severely burned sites was more heterogeneous (Figure 4.1a). Patchy distributions of *Populus tremuloides* within one site, and *Epilobium angustifolium* within another site, were responsible for the differences within severely burned sites, while *Spiraea betulifolia* was associated with differences in seed bank species composition within logged sites (ISA: $p < 0.05$; Table 4.1). On logged sites and severely burned sites, 63% and 60% (respectively) of the within-grid plots did not contain any seeds, so fewer pair-

wise comparisons among grids were possible here than within lightly burned and undisturbed sites (see values on top of within-site bars in Figure 4.1a). Thus, in addition to the heterogeneity in species composition found using MRPP, there was further heterogeneity in simple presence/absence of seeds, especially within logged and severely burned sites.

Figure 4.1. Heterogeneity index (proportion of significantly different pair-wise comparisons: MRPP, $p < 0.05$; actual numbers given above each bar) for (a) seed bank and (c) vegetation communities among and within undisturbed (UN), lightly burned (LB), severely burned (SB) and logged (CC) sites, and for (b) seed bank versus vegetation communities on sites and within-site grids.
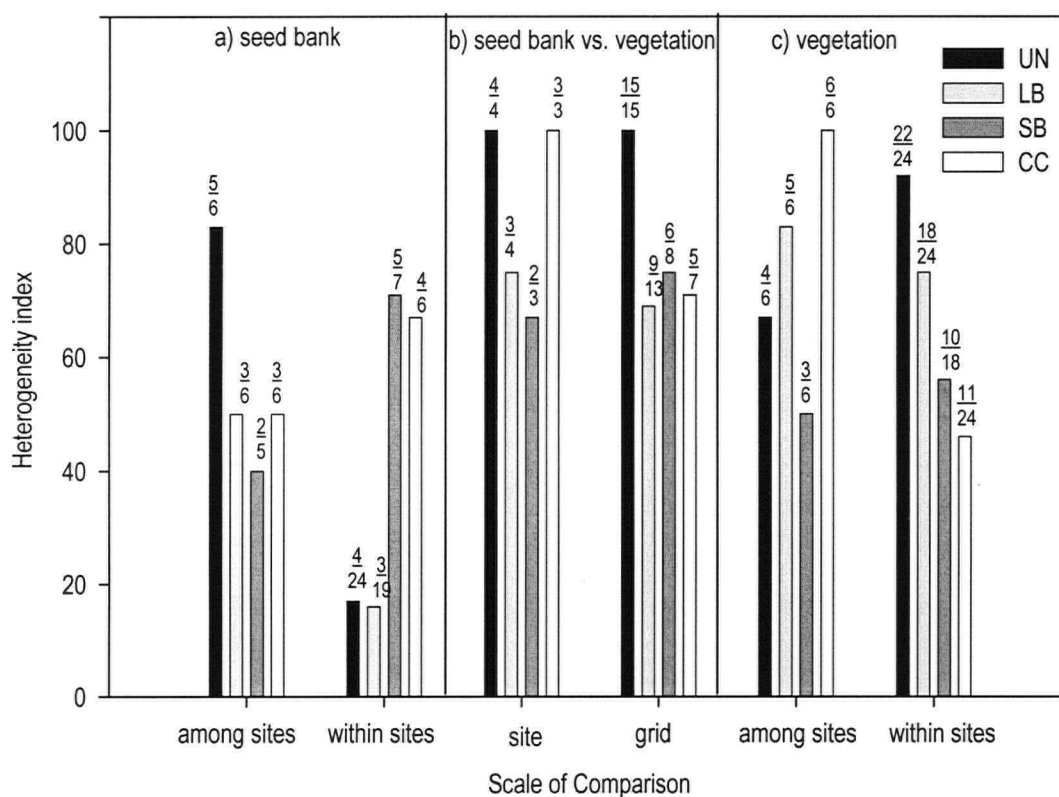
Table 4.1. Number of seeds of each species present in the seed bank on (SITE: Ash = Ashcroft, Oli = Oliver, Leo = Leonie, and Jam = Jamieson) and within (GRID: letters denote direction of grid from site centre) undisturbed (a), lightly burned (b), severely burned (c), and logged (d) sites. Species associated with differences in seed bank species composition (ISA: $p < 0.05$) are indicated with [a] for among-site differences and [w] for within-site differences.

a)

UN seed bank Species	SITE Ash	Oli	Leo	Jam	GRID Ash N	E	S	W	Oli N	E	S	W	Leo N	E	S	W	Jam N	E	S	W
Antennaria neglecta	6							6												
Antennaria pulcherrima		4											1		1	2				
Antennaria racemosa	1											1								
Aquilegia formosa	1					1														
Arabis holboellii	13					4	1	8												
Betula papyrifera [a]		11	29	6					2	1	5	3	8	12	3	6	1	2	1	2
Carex sp. [w]	3	5		1	1	1		1		4	1						1			
Cerastium fontanum		5										5								
Cirsium vulgare		1	4								1		2		2					
Collinsia parviflora	6							6												
Conyza canadensis		1													1					
Epilobium angustifolium	1	3	1		1									1	1	1				1
Epilobium ciliatum [w]	6	1	5		2		1	3								1	2	2	1	
Filago arvensis		2											1	1						
Fragaria vesca		4	3	2					1	1		2			3	1				1
Fragaria virginiana		1														1				
Galium triflorum		8		10					1		2	5							8	2
Hieracium umbellatum		1														1				
Juncus bufonius		1		1					1											1
Lathyrus sp.		1											1							
Paxistima myrsinites	3	2				2		1					1	1						
Picea sp.		1																		1
Plantago major		1							1											
Poa sp.	22	2			4	13	1	4			2									
Populus tremuloides	1	7	1					1						3	1	3				1
Potentilla diversifolia		1													1					
Ribes lacustre		2							2											
Rubus idaeus		5	2						1	3	1			2						
Rubus parviflorus		1		5										1			1		2	2
Salix sp.		1		1					1										1	
Sedum lanceolatum	32						5	27												
Sonchus arvensis	1				1															
Taraxacum officinale	1				1															
Typha latifolia			2	1											1		1		1	
Verbascum thapsus		2							1	1										
Viola sp. [a]		6							1	1	1	3								

b)

LB seed bank Species	SITE Ash	Oli	Leo	Jam	GRID Ash N	E	S	W	Oli N	E	S	W	Leo N	E	S	W	Jam N	E	S	W
Antennaria racemosa		1		1								1								1
Arabis holboellii	8						7	1												
Asteraceae	3					1	2													
Betula papyrifera		2								1	1									
Carex sp.	1							1												
Collinsia parviflora	3					1	2													
Epilobium angustifolium	2	3	2	1	1	1			1	1	1				1	1				1
Epilobium ciliatum		1	2	1							1		2						1	
Mitella nuda				27													1	26		
Poa sp.	5				1	1		3												
Populus tremuloides [a]		1	8	6									1	1	2	1	4	3	2	1
Pseudotsuga menziesii	1		1		1									1						
Salix sp.				1															1	
Shepherdia canadensis		1									1									
Typha latifolia	1		1	1								1					1	1		
Vicia americana				1															1	

c)

SB seed bank	SITE				GRID															
					Ash				Oli				Leo				Jam			
Species	Ash	Oli	Leo	Jam	N	E	S	W	N	E	S	W	N	E	S	W	N	E	S	W
Antennaria pulcherrima		1							1											
Asteraceae	1					1														
Carex sp.	1			3	1														3	
Epilobium angustifolium [w]			3	9									1	2			5	4		
Epilobium ciliatum			4										3		1					
Poa sp.	1							1												
Populus tremuloides [aw]			16	2									8	1	1	6			2	
Salix sp.		2	1						1	1			1							
Spiraea betulifolia			4																4	

d)

CC seed bank	SITE				GRID															
					Ash				Oli				Leo				Jam			
Species	Ash	Oli	Leo	Jam	N	E	S	W	N	E	S	W	N	E	S	W	N	E	S	W
Anethum graveolens				1																1
Antennaria pulcherrima		1												1						
Betula papyrifera			2															1	1		
Carex sp.	1	1	1						1	1					1					
Cerastium fontanum	1						1													
Epilobium angustifolium			1																1	
Epilobium ciliatum			3																2	1
Fragaria vesca		3												3						
Linnaea borealis			1																	1
Plantago major		1												1						
Populus tremuloides		1													1					
Rubus idaeus			1															1		
Sagina apetala		1												1						
Salix sp.		1										1								
Sedum lanceolatum		2													2					
Spiraea betulifolia [w]		10	22									10	11		1	10				
Typha latifolia			1																1	

4.2.2 Vegetation vs. seed bank, and vegetation heterogeneity at different scales

Seed bank communities differed from vegetation communities on and within all undisturbed sites, while in most cases fewer differences occurred both on and within disturbed sites (Figure 4.1b). In the vegetation (Figure 4.1c), four of the six pair-wise comparisons among undisturbed sites showed differences in species composition, but this trend was driven by one site being different from the other three; when this site was removed from the analysis, the vegetation communities on undisturbed sites appeared to be more similar to each other (not shown). Vegetation communities within the undisturbed sites were more heterogeneous than they were among sites (Figure 4.1c). Among-site heterogeneity in vegetation species composition increased from undisturbed to lightly burned to logged sites, while severely burned sites showed the least among-site heterogeneity. Within-site heterogeneity decreased from undisturbed sites to lightly burned sites, to severely burned sites, to logged sites (Figure 4.1c). In Table 4.2, much of the within- and among-site heterogeneity discussed above is evident, and indicator species associated with the differences are given.

Table 4.2. Species present in vegetation communities on (SITE: Ash = Ashcroft, Oli = Oliver, Leo = Leonie, and Jam = Jamieson) and within (GRID: letters denote direction of grid from site centre) undisturbed (a), lightly burned (b), severely burned (c), and logged (d) sites. Values denote # occupied 10 cm x 10 cm subplots - a maximum of 400 was possible at the site scale, and a maximum of 100 was possible at the grid scale. Species associated with differences in vegetation species composition (ISA: $p < 0.05$) are indicated with [a] for among-site differences and [w] for within site differences.

a)

UN vegetation Species	SITE Ash	Oli	Leo	Jam	GRID Ash N	E	S	W	Oli N	E	S	W	Leo N	E	S	W	Jam N	E	S	W
Achillea millefolium	3						2	1												
Agropyron spicatum			11																	11
Allium cernuum	82				49	29		4												
Amelanchier alnifolia	1	3			1								2	1						
Arabis holboellii	7					1		6												
Aralia nudicaulis		4											4							
Arctostaphylos uva-ursi	37				25	2	3	7												
Arnica cordifolia	137	31			40	47	49	1		3	12	16								
Aster sp.	4	1	5			4							1						2	3
Astragalus sp.	25				2		6	17												
Calamagrostis rubescens [w]	152	78	69	111	47	35	45	25	31	28	7	12	19			50	20		48	43
Carex sp.	94				41	3	37	13												
Chimaphila umbellata [a]			93										47	8	12	26				
Clematis occidentalis		1								1										
Clintonia uniflora [w]			2	18									2							18
Collinsia parviflora	55						2	53												
Cornus canadensis [w]			30										18	6		6				
Cornus stolonifera		3												3						
Disporum hookeri		6							2		2	2								
Epilobium angustifolium		1		1					1									1		
Erigeron sp.	1							1												
Fragaria vesca		15	2	2					5	9		1	2						2	
Fragaria virginiana	7				6	1														
Galium boreale				1															1	
Galium triflorum		10		6						3		7							2	4
Goodyera oblongifolia	5		4	20	5								1	2		1	10		8	2
Hieracium albiflorum		6	1						6							1				
Lathyrus sp.		4		14					2	1		1							9	5
Linnaea borealis [w]		60	89	140					13	38	9		35	24	1	29	1		65	74
Mahonia aquifolium [a]	13	1	9		6	7				1			3	2	1	3				
Orthilia secunda			7	25									5	1		1			10	15
Osmorhiza chilensis [w]				29															13	16
Paxistima myrsinites [w]		21	32	33						7	14		20	6		6	6		14	13
Pedicularis bracteosa		5							5											
Poa sp.	9						6	1	2											
Pseudotsuga menziesii		4	8	1						2	1	1		2	2	4	1			
Ranunculus sp.		1							1											
Rosa sp.	4	6	3		4				5	1						3				
Rubus parviflorus		2	2													2			2	
Rubus sp.		12	3	5					4	4		4	3						3	2
Sedum lanceolatum	6						1	5												
Smilacina racemosa		1		5											1				1	4
Spiraea betulifolia		21	5	20					2	3	10	6		4	1	5			8	7
Symphoricarpos albus		9		1					7	2						1				
Taraxacum officinale [a]		1							1											
Thalictrum occidentale				6															6	
Vaccinium sp.				1															1	
Viola adunca			1										1							

b)

LB vegetation	SITE				GRID Ash				Oli				Leo				Jam			
Species	Ash	Oli	Leo	Jam	N	E	S	W	N	E	S	W	N	E	S	W	N	E	S	W
Achillea millefolium	14					1	10	3												
Agropyron sp.	24				9	5	10													
Allium cernuum	40			48		4	11	25									19		25	4
Antennaria sp.		2		14							1					1	3		4	7
Arabis holboellii	29						25	4												
Arctostaphylos uva-ursi			1										1							
Arnica cordifolia [w]	10	2	1	49	4			6		2						1	19		12	18
Aster sp.	1			4		1														4
Astragalus sp.	1							1												
Betula papyrifera				5													3			2
Calamagrostis rubescens [w]	40	28	37	77	12	8	18	2		10	1	18	23			14	48		1	28
Carex sp.	21	1	5				17	4		1							1		1	3
Cirsium vulgare		1		1								1				1				
Collinsia parviflora	82			6		24	53	5											6	
Cornus stolonifera			49						9	1						39				
Epilobium angustifolium [w]	13	205	208	167	11		2		45	39	75	46	32	83	75	18	12	65	39	51
Epilobium ciliatum		2	4											2	3	1				
Erigeron sp.	1						1													
Fragaria vesca	5						5													
Fragaria virginiana				2													1		1	
Goodyera oblongifolia			1													1				
Linnaea borealis			7													6	1			
Mahonia aquifolium			1													1				
Paxistima myrsinites			13													13				
Polygonum douglasii	22						22													
Populus tremuloides [aw]		2	47	99					1			1	3	11	23	10	6	33	26	34
Pseudotsuga menziesii [a]	19	14	109	36	15		2	2	1	2	5	6	15	38	38	18	1	21	6	8
Rosa sp.	1	1	10	2			1					1	4	1	1	4	1		1	
Rubus sp.				9													6		2	1
Sedum lanceolatum	1						1													
Spiraea betulifolia	26	2	14	28	1	24		1		2			5	3	2	4	12		7	9
Symphoricarpos albus				5															5	
Taraxacum officinale	1						1													
Tragopogon dubius	2						2													

c)

SB vegetation	SITE				GRID Ash				Oli				Leo				Jam			
Species	Ash	Oli	Leo	Jam	N	E	S	W	N	E	S	W	N	E	S	W	N	E	S	W
Allium cernuum	3						3													
Arctostaphylos uva-ursi	4					1	3													
Arnica cordifolia [a]	20	1	1	20	2	1	17			1						1	3	6	1	10
Astragalus sp.	2				1		1													
Balsamorhiza sagittata	5						5													
Betula papyrifera				6															6	
Calamagrostis rubescens [w]	19	24	13	44	12		7		10	10	1	3		8		5	30	1		13
Carex sp.	63	8	1	2	3	37	23		3	1		4				1			2	
Cirsium vulgare			1													1				
Collinsia parviflora	27					8	19													
Epilobium angustifolium [aw]		30	143	34					4	9		17	43	55	27	18	23	11		
Epilobium ciliatum			1													1				
Lathyrus sp.				1																1
Paxistima myrsinites		5							3	1	1									
Polygonum douglasii	6						6													
Populus tremuloides [a]			42										16	17	6	3				
Pseudotsuga menziesii [a]			18	10									1	13	2	2	2	5	3	
Rosa sp.				1													1			
Spiraea betulifolia		8	10	1					3			5	4	1			5		1	
Symphoricarpos albus	16			1		4	12													1
Tragopogon dubius	2						2													
Vaccinium sp.			1																1	
Vicia americana				1															1	

d)

CC vegetation / Species	SITE Ash	Oli	Leo	Jam	GRID Ash N	E	S	W	Oli N	E	S	W	Leo N	E	S	W	Jam N	E	S	W
Amelanchier alnifolia			3										3							
Antennaria sp.		1										1								
Aquilegia formosa			1										1							
Aralia nudicaulis w			34										11	23						
Arctostaphylos uva-ursi	3						3													
Arnica cordifolia	27	1		7	7	3	17		1										7	
Aster sp.		3	2									3		2						
Calamagrostis rubescens w	149	13	54	64	13	45	40	51		7		6	15	9	23	7			64	
Carex sp.	3	5				1	2		1		2	2								
Chimaphila umbellata				15														2	9	4
Cirsium vulgare		1							1											
Clintonia uniflora			16										2	14						
Cornus canadensis w			50										16	30	4					
Epilobium angustifolium	5	14	24	8	4		1		8	5		1	5		6	13	3	1	1	3
Epilobium ciliatum				1															1	
Galium boreale	3				3															
Linnaea borealis	9	2	9	14		5		4				2			9		2	3	6	3
Mahonia aquifolium			3	8									3				2			6
Medicago sativa a		15							3	7	3	2								
Orthilia secunda	8				4	1		3												
Osmorhiza chilensis			5	6									3	2					6	
Paxistima myrsinites		7		40					6	1							18	4	7	11
Populus tremuloides		1	1	1								1	1						1	
Pseudotsuga menziesii		3	1	1						1	2					1	1			
Rosa sp.	6	4	8				6					4	5			3				
Salix sp.		1												1						
Shepherdia canadensis	8				8															
Smilacina racemosa				4																4
Spiraea betulifolia		9	21	10					1		1	7	8	3	2	8			10	
Symphoricarpos albus				1																1
Vaccinium sp.	12		9	6				12					4	1	4			3		3

4.2.3 Effectiveness of seed bank sampling

A total of 41 species was sampled in the soil seed bank on undisturbed sites, and the first-order jackknife estimate of 55 species suggests that only 75% of species actually present were detected on these sites (Figure 4.2). The seed bank sampling scheme was more effective on lightly burned sites, where the 19 sampled species comprised 83% of the estimated total of 23 species. Only eleven species occurred in seed bank samples on severely burned sites, but jackknife estimates suggest that this was 74% of the estimated total of 14 species. The 19 species sampled on logged sites represented only 63% of the estimated total of 30 species. Moreover, the species-area curve for logged sites showed the least indication of all disturbance types of approaching a plateau (Figure 4.2). Species-area curves were generated to determine the number of samples required to account for all of the species sampled in the seed bank. Because none of the species-area curves reached a plateau, more than the 240 samples collected per disturbance class are required to accurately characterize the seed bank.

Figure 4.2. Average number of species that occurred in randomly generated groups of soil seed bank samples ranging in size from 1 to 147 samples on undisturbed (UN) sites, from 1 to 69 samples on lightly burned (LB) sites, from 1 to 39 samples on severely burned (SB) sites, and from 1 to 42 samples on logged (CC) sites (the remainder of the samples did not contain any seeds). Values at the end of each curve indicate: (actual # species present) / (jackknife estimate of # species present).
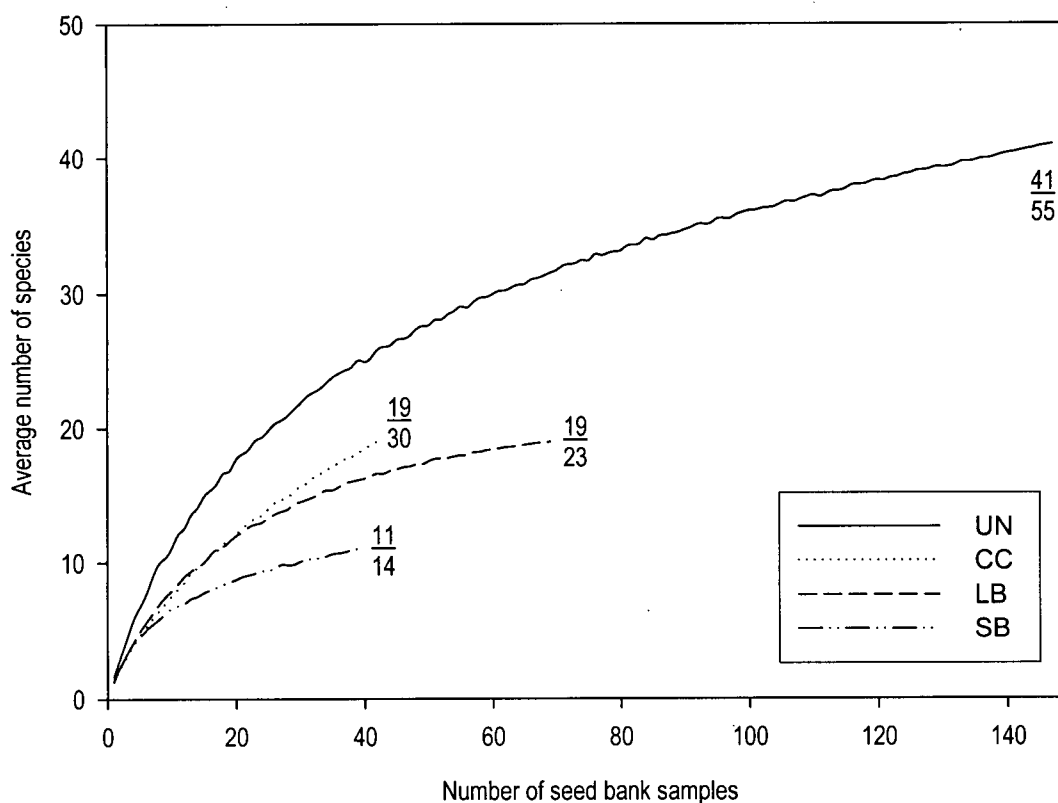
4.3 Discussion

4.3.1 Heterogeneity in undisturbed soil seed banks

Many ecologists have discussed the role of the soil seed bank as an inter-disturbance species storage reservoir (e.g. Harper 1977; Thompson and Grime 1979). Rather than holding a common assortment of species on all sites, the seed bank in mature IDF forest stands contained a smattering of species that combined to form unique communities on all except one pair of undisturbed sites. Although few studies of forest soil seed banks have explicitly documented horizontal spatial structure (Matlack and Good 1990; Olano et al. 2002), large variances associated with seed density estimates suggest that heterogeneity in seed distribution both among and within sites is common (Archibold 1979; Pratt et al. 1984; Morgan and Neuenschwander 1988).

The suite of species present in seed bank communities on undisturbed sites indicates that the seed bank is a result of past (species not present in the vegetation, e.g. *Ribes lacustre*), ongoing (species whose seeds remain viable for less than one year, e.g. *Betula papyrifera*), proximal (species present in the vegetation with no known adaptations for long distance dispersal, e.g. *Paxistima myrsinites*), and distal (species from other vegetation zones, e.g. *Typha latifolia*) seed dispersal processes. Heterogeneity in seed bank species composition among sites could be the result of among-site variation in the above seed dispersal processes (Jacquemyn et al. 2003), site-specific post-dispersal seed movements (Hulme 1998), or different local biotic or abiotic factors affecting seed dormancy and/or persistence in the soil (Baskin and Baskin 1998). Seed bank species composition was more consistent within undisturbed forest sites than it was among these sites. Many species were found on all or almost all grids within a site, and their widespread occurrence is the result of either dispersal abilities allowing seed movements of 15 m or more, or a local abundance of seed sources in past or present vegetation communities.

4.3.2 Post-disturbance seed and seedling distributions

In addition to the seed density estimates provided by greenhouse germination trials, information regarding seed availability and spatial heterogeneity on disturbed sites can be gleaned from accounts of seedling distributions in the establishing vegetation communities in close spatial proximity to seed bank sample origin. Seedlings of *Epilobium angustifolium*, *Populus tremuloides*, and *Pseudotsuga menziesii* occurred in high numbers in both seed bank samples and establishing vegetation communities on most burned sites. The widespread presence of these wind-dispersed species is not surprising since such species often have high fecundities and good long distance dispersal abilities (Clark et al. 1998). The occurrence of *Epilobium angustifolium* and *Pseudotsuga menziesii* seedlings on all grids within all lightly burned sites indicates that seed sources were regionally and locally available following fires of this severity. In severely burned areas, the presence of *Epilobium angustifolium* seedlings on all sites, but the absence of seedlings of this

species on some within-site grids indicates that seed dispersal was limited for this species at a local scale. In contrast, *Pseudotsuga menziesii* seedlings occurred on only one severely burned site, but they were frequent on all grids within that site. Seed sources were thus limited at a larger scale, but when present, seed production was sufficient to cover the site with seeds. Although seeds dispersed by animals (either through ingestion or adhesion) often have greater migration rates than wind-dispersed seeds (Matlack 1994; Takahashi and Kamitani 2004), the limitation of zoochores such as *Fragaria virginiana*, *Ribes lacustre* and *Rubus parviflorus* to seed bank communities on undisturbed sites in this study suggests that species employing this mode of dispersal had not yet colonized disturbed sites.

4.3.3 Heterogeneity in seed bank and vegetation species composition

The patterns of seed bank heterogeneity observed among the undisturbed sites sampled here had more than a century to develop. On disturbed sites, large portions of the forest floor (which contains the majority of the seed bank) were either removed or disrupted by the disturbances, and the resulting seed bank communities contained fewer species and were less heterogeneous among sites than were those in undisturbed areas. A combination of disturbance removing pre-existing heterogeneity and dispersal adding the seeds of a few prolific seed producers to most sites was likely responsible for the lower level of heterogeneity in seed bank species composition among disturbed sites compared to among undisturbed sites. High levels of heterogeneity in seed bank species composition within logged and severely burned sites likely resulted from limited seed availability and dispersal at that scale (Greene and Johnson 1996; Turner et al. 1998).

Plants of seed origin made only a minor contribution to the vegetation communities that established on logged sites (Chapter 3). Therefore, among-site differences in vegetation species composition on logged sites probably resulted from site-level differences in the effects of logging on root propagules combined with the absence of homogenizing seed dispersal events by prolific seed dispersers (Clark et al. 1998). In contrast, plants of seed origin made a larger contribution to establishing vegetation communities on lightly burned and severely burned sites (Chapter 3), and the presence of these species probably contributed to the lower levels of heterogeneity in vegetation species composition among sites (Clark et al. 1998). Within disturbed sites, local dominance and local dispersal of a few species (Chambers and MacMahon 1994; Turner et al. 1998) resulted in lower species richness and more homogeneous vegetation communities than within neighbouring undisturbed sites.

In mature forest stands, the species composition of the soil seed bank generally differs from that of the vegetation (Warr et al. 1993), and at all spatial scales examined here, seed bank and vegetation communities on undisturbed sites had significantly different species compositions. In recently disturbed areas where a large component of the vegetation is establishing from seed, a

closer correspondence between seed bank and vegetation communities is expected (Decocq et al. 2004). As described in Chapter 3, this close correspondence between seed bank and vegetation was found on severely burned sites, but seed bank and vegetation communities were different on lightly burned and logged sites. In this chapter, analysis at finer scales revealed that seed bank and vegetation communities on one lightly burned site and four lightly burned grids did not differ, and that while differences between seed bank and vegetation communities persisted at the site scale in logged areas, within sites, two grids did not differ. Patches of seed-derived vegetation that are similar in species composition to the seed bank therefore seem to occur at finer spatial scales than those considered in Chapter 3. To account for this variability, scale of sample collection and data analysis should be considered carefully when making this type of comparison in recently disturbed areas.

4.3.4 Effectiveness of seed bank sampling and methodological considerations

Because the sampling design was initially considered adequate to fully describe the seed bank, all species were expected to be accounted for and species-area curves were expected to plateau. Contrary to expectation, jackknife estimates of actual numbers of species in the seed bank, and slopes of species-area curves indicated that seed bank sampling did not account for all of the species that were actually present on the study sites. If a species were i) not collected from a site, or ii) collected but unable to germinate under available conditions then it would not have been detected in this study. The inclusion of sixteen sites with four replicate sites per disturbance class and four sampling grids within each site reflected one of the overall study objectives of describing seed bank species assemblages at a variety of spatial scales following different types of disturbance. Unfortunately, this experimental design combined with limitations in available greenhouse space allowed only 0.15 m^2 of soil to be collected from each site. Given the low seed densities of many species in forest soils (Clark et al. 1999), it is possible that 0.15 m^2 of soil was not sufficient to detect all of the species on each site. Although the conditions provided in the greenhouse stimulated the germination of forty-eight species, the possibility that ungerminated seeds remained in soil samples following natural and artificial stratification and 18 weeks in the greenhouse cannot be ruled out.

Species-area curves and jackknife estimates were based on only those seed bank samples that contained seeds; however, empty samples were common in this study. On undisturbed sites, for approximately every two samples collected, only one contained seeds. In lightly burned areas, three samples were empty for every one that contained seeds, and on severely burned and logged sites the ratio of empty to non-empty seed bank samples was 6:1. When these large proportions of the 960 collected samples that were empty are taken into consideration, the feasibility of carrying out a study that accounts for all species present becomes questionable. To account for some of the

among-site variation in seed bank species composition described here, multiple stands should be sampled when one is characterizing the soil seed bank in mature, undisturbed forests. When sampling in recently disturbed areas, more within-site samples than the 60 collected for this study are required to account for within-site variation in seed bank species composition, particularly in logged and severely burned areas.

5. SUMMARY AND CONCLUSIONS

This thesis presents the first systematic account of soil seed bank response to fire and logging in the IDF forests of BC. Baseline information on seed density, species richness, and species composition of soil seed banks is useful to land managers because seed banks can contain the seeds of both desirable and undesirable species. Knowledge of seed bank species composition should be obtained before using soil seed banks for restoration purposes. The seed banks sampled here contained 74 taxa; sixteen of these were species not native to North America.

Within the first year following low severity fire, high severity fire, and logging, soil seed banks contained fewer seeds and fewer total species, and had different species compositions than those in neighbouring undisturbed areas. While the seed banks of disturbed areas were similar to each other in this respect, the frequency of seed-origin plants in establishing vegetation communities decreased in the order: lightly burned > severely burned > logged. The inferred post-disturbance arrival of *Epilobium angustifolium*, *Populus tremuloides*, *Pseudotsuga menziesii*, and *Salix* spp. in high numbers on burned sites, and the scarcity of seeds or seedlings of these taxa on logged sites, indicates that they were limited in their abilities to disperse into large openings created by logging.

Although few data supporting its effectiveness exist, broadcast seeding of non-native annual or perennial grass species is sometimes carried out in burned areas to prevent soil erosion (Beschta et al. 2004; Beyers 2004). While the effects of disturbance on soil structure and the potential for erosion were not examined in this study, the extent to which natural vegetation recovery took place on lightly burned and severely burned sites suggests that broadcast seeding might not be necessary following fire in this system. On logged sites, given the low total frequency of establishing vegetation and the scarcity of post-disturbance seed arrivals, seeding of native species might speed recovery of the native flora. Addition of non-native species could result in the displacement of native species, including desired conifer species (Beyers 2004), and should only be considered if the management goal is to encourage the growth of cattle forage species or to alter the ecosystem for other reasons.

The undisturbed forest stands sampled here were characterized by different seed bank communities. The existence of such heterogeneity suggests that multiple stands need to be sampled in order to accurately describe seed bank species composition in this type of forest. Disturbance appears to generate greater patchiness in seed banks on severely burned and logged sites, both in terms of seed presence/absence and species composition when seeds were present. Intensive, within-stand sampling would be required to account for the full range of heterogeneity present. The collection of many small soil samples has been advocated as an effective means of accounting for much of the inherent variation in soil seed bank structure (Bigwood and Inouye 1988; Thompson 1986; Warr et al. 1993). Even though 960 25 cm^2 soil samples were collected to represent the seed

bank in IDF forests (240 samples per disturbance class), species-area curves and jackknife estimates of total species richness suggest that this number of samples was insufficient to account for all species actually present.

The relationship between seed bank and vegetation communities on sites disturbed five and ten years prior to sampling suggests that the major contribution of the seed bank is made soon after disturbance; as time since disturbance increased, the number of species shared by seed bank and vegetation communities decreased. Five years after disturbance by fire and ten years after disturbance by logging, there were no significant differences in species composition of either seed bank or vegetation communities between disturbed and corresponding undisturbed areas, suggesting that seed bank and vegetation communities can recover from either fire or logging disturbance fairly quickly. Long-term studies on the success of natural and planted conifer seedlings, as well as changes in plant community composition over longer time scales are required to complement this study and increase our understanding of vegetation dynamics following disturbance by fire and logging in IDF forests.

LITERATURE CITED

Agee, JK. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington DC. 493 pp.

Anon. 2000. SYSTAT version 10. SPSS Inc.

Archibold, OW. 1979. Buried viable propagules as a factor in postfire regeneration in northern Saskatchewan. Canadian Journal of Botany 57: 54-58.

Arsenault, A and W Klenner. 2004. Fire regime in dry-belt forests of British Columbia: perspectives on historic disturbances and implications for management. *In* Mixed Severity Fire Regimes: Ecology and Management conference proceedings, Spokane, Washington. (www.emmps.wsu.edu/fire)

Arseneault, D. 2001. Impact of fire behavior on postfire forest development in a homogeneous boreal landscape. Canadian Journal of Forest Research 31: 1367-1374.

Baskin, CC and JM Baskin. 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, San Diego.

Beatty, SW. 1991. Colonization dynamics in a mosaic landscape: the buried seed pool. Journal of Biogeography 18: 553-563.

Beschta, RL, JJ Rhodes, JB Kauffman, RE Gresswell, GW Minshall, JR Karr, DA Perry, FR Hauer, and CA Frissell. 2004. Postfire management on forested public lands of the western United States. Conservation Biology 18: 957-967.

Beyers, JL. 2004. Postfire seeding for erosion control: effectiveness and impacts on native plant communities. Conservation Biology 18: 947-956.

Bigwood, DW, and DW Inouye. 1988. Spatial pattern analysis of seed banks: an improved method and optimized sampling. Ecology 69: 497-507.

Brown, D. 1992. Estimating the composition of a forest seed bank: a comparison of the seed extraction and seedling emergence methods. Canadian Journal of Botany 70: 1603-1612.

Chambers, JC, and JA MacMahon. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics 25: 263-292.

Chrosciewicz, Z. 1974. Evaluation of fire-produced seedbeds for jack pine regeneration in central Ontario. Canadian Journal of Forest Reserach 4: 455-457.

Clark, DL and MV Wilson. 1994. Heat-treatment effects on seed bank species of an old-growth Douglas-fir forest. Northwest Science 68: 1-5.

Clark JS, E Macklin, and L Wood. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. Ecological Monographs 68: 213-235.

Clark, JS, B Beckage, P Camill, B Cleveland, J HilleRisLambers, J Lichter, J McLachlan, J Mohan, and P Wyckoff. 1999. Interpreting recruitment limitation in forests. American Journal of Botany 86: 1-16.

Coffin, DP, and WK Lauenroth. 1989. Spatial and temporal variation in the seed bank of a semiarid grassland. American Journal of Botany 76: 53-58.

Decocq, G, B Valentin, B Toussaint, F Hendoux, R Saguez, and J Bardat. 2004. Soil seed bank composition and diversity in a managed temperate deciduous forest. Biodiversity and Conservation 13: 2485-2509.

Donelan, M, and K Thompson. 1980. Distribution of buried viable seeds along a successional series. Biological Conservation 17: 297-311.

Duchesne, LC. 1994. Fire and biodiversity in temperate ecosystems. In: Biodiversity, temperate ecosystems and global change. Edited by: TJB Boyle and CEB Boyle. Springer-Verlag, New York.

Dufrêne, M and P Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345-366.

Dyrness, CT, and RA Norum. 1983. The effects of experimental fires on black spruce forest floors in interior Alaska. Canadian Journal of Forest Research 13: 879-893.

Egler, FE. 1954. Vegetation science concepts I. Initial floristic composition. A factor in old-field vegetation development. Vegetatio 4: 412-417.

Forcella, F. 1984. A species-area curve for buried viable seeds. Australian Journal of Agricultural Research 35: 645-652.

Fyles, JW. 1989. Seed bank populations in upland coniferous forests in central Alberta. Canadian Journal of Botany 67: 274-278.

Granström, A. 1987. Seed viability of fourteen species during five years of storage in a forest soil. The Journal of Ecology 75: 321-331.

Granström, A. 1982. Seed banks in five boreal forest stands originating between 1810 and 1963. Canadian Journal of Botany 60: 1815-1821.

Greene, DF, and EA Johnson. 1996. Wind dispersal of seeds from a forest into a clearing. Ecology 77: 595-609.

Greene, DF, JC Zasada, L Sirois, D Kneeshaw, H Morin, I Charron, and M-J Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Canadian Journal of Forest Research 29: 824-839.

Gross, KL. 1990. A comparison of methods for estimating seed numbers in the soil. Journal of Ecology 78: 1079-1093.

Harper, JL. 1977. Population Biology of Plants. Academic Press, London.

Henderson, CB, KE Petersen, and RA Redak. 1988. Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. Journal of Ecology 76: 717-728.

Huggard, DJ, A Arsenault, A Vyse, and W Klenner. 2005. The Opax Mountain Silvicultural Systems Project: preliminary results for managing complex, dry Interior Douglas-fir forests. BC Ministry of Forests Extension Note 72.

Hughes, JW, and DA Bechtel. 1997. Effect of distance from forest edge on regeneration of red spruce and balsam fir in clearcuts. Canadian Journal of Forest Research 27: 2088-2096.

Hulme, PE. 1998. Post-dispersal seed predation and seed bank persistence. Seed Science Research 8: 513-519.

Hyatt, LA. 1999. Differences between seed bank composition and field recruitment in a temperate zone deciduous forest. American Midland Naturalist 142: 31-38.

Ingersoll, CA, and MV Wilson. 1990. Buried propagules in an old-growth forest and their response to experimental disturbances. Canadian Journal of Botany 68: 1156-1162.

Inouye, RS. 1980. Density-dependent germination response by seeds of desert annuals. Oecologia 46: 235-238.

Jacquemyn, H, J Butaye, and M Hermy. 2003. Influence of environmental and spatial variables on regional distribution of forest plant species in a fragmented and changing landscape. Ecography 26: 768-776.

Kellman, MC. 1970. The viable seed content of some forest soil in coastal British Columbia. Canadian Journal of Botany 48: 1383-1385.

Kellman, MC. 1974. Preliminary seed budgets for two plant communities in coastal British Columbia. Journal of Biogeography 1: 123-133.

Klenner, W and A Vyse. 1998. The Opax Mountain Silviculture Systems Project: evaluating alternative approaches to managing dry Douglas-fir forests. In Managing the dry Douglas-fir forests of the southern Interior: workshop proc. A Vyse, C Hollstedt, and D Huggard (editors). BC Ministry of Forests, Victoria, BC. Work. Pap. 34/1998.

Kramer, NB, and FD Johnson. 1987. Mature forest seed banks of three habitat types in central Idaho. Canadian Journal of Botany 65: 1961-1966.

Kropáč, Z. 1966. Estimation of weed seeds in arable soil. Pedobiologia 6: 105-128.

Landenberger, RE and JB McGraw. 2004. Seed-bank characteristics in mixed-mesophytic forest clearcuts and edges: Does "edge effect" extend to the seed bank? Canadian Journal of Botany 82: 992-1000.

Lee, P. 2004. The impact of burn intensity from wildfires on seed and vegetative banks, and emergent understory in aspen-dominated boreal forests. Canadian Journal of Botany 82: 1468-1480.

Livingston, RB, and ML Allessio. 1968. Buried viable seed in successional field and forest stands, Harvard Forest, Massachusetts. Bulletin of the Torrey Botanical Club 95: 58-69.

Lloyd, D, K Angove, G Hope, and C Thompson. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. BC Ministry of Forests, Victoria BC.

Lortie, CJ, and R Turkington. 2002. The small-scale spatiotemporal pattern of a seed bank in the Negev Desert, Israel. Écoscience 9: 407-413.

Matlack, GR, and RE Good. 1990. Spatial heterogeneity in the soil seed bank of a mature Coastal Plain forest. Bulletin of the Torrey Botanical Club 11: 143-152.

Matlack, GR. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology 75: 1491-1502.

McCune, B, and MJ Mefford. 1999. Multivariate Analysis of Ecological Data, Version 4.17. MjM Software, Gleneden Beach, Oregon, USA.

McCune, B, JB Grace, and DL Urban. 2002. Analysis of Ecological Communities. MjM Software Design. Gleneden Beach, Oregon, USA. 300 pp.

McGee, A, and MC Feller. 1993. Seed banks of forested and disturbed soils in southwestern British Columbia. Canadian Journal of Botany 71: 1574-1583.

McLean, A. 1967. Germination of forest range species from southern British Columbia. Journal of Range Management 20: 321-322.

McLean, A. 1969. Fire resistance of forest species as influenced by root systems. Journal of Range Management 22: 120-122.

Moore, JM, and RW Wein. 1977. Viable seed populations by soil depth and potential site recolonization after disturbance. Canadian Journal of Botany 55: 2408-2412.

Morgan, P, and LF Neuenschwander. 1988. Seed-bank contributions to regeneration of shrub species after clear-cutting and burning. Canadian Journal of Botany 66: 169-172.

Murray, BR. 1998. Density-dependent germination and the role of seed leachate. Australian Journal of Ecology 23: 411-418.

Olano, JM, I Caballero, NA Laskurain, J Loidi, and A Escudero. 2002. Seed bank spatial pattern in a temperate secondary forest. Journal of Vegetation Science 13: 775-784.

Olmsted, NW, and JD Curtis. 1947. Seeds of the forest floor. Ecology 28: 49-52.

Oosting, HJ, and ME Humphreys. 1940. Buried viable seeds in a successional series of old-field and forest soils. Bulletin of the Torrey Botanical Club 67: 253-273.

Owen, NW, M Kent, and MP Dale. 2001. Spatial and temporal variability in seed dynamics of machair sand dune plant communities, the Outer Hebrides, Scotland. Journal of Biogeography 28: 565-588.

Parker, WC, SR Watson, and DW Cairns. 1997. The role of hair-cap mosses (*Polytrichum* spp.) in natural regeneration of white spruce (*Picea glauca* (Moench) Voss). Forest Ecology and Management 92: 19-28.

Pausas, JG, RA Bradstock, DA Keith, JE Keeley, and the GCTE (Global Change of Terrestrial Ecosystems) Fire Network. 2004. Plant functional traits in relation to fire in crown-fire ecosystems. Ecology 85: 1085-1100.

Peterson, DL, and KC Ryan. 1986. Modeling post-fire conifer mortality for long-range planning. Environmental Management 10: 797-808.

Pisaric, MFJ. 2002. Long-distance transport of terrestrial plant material by convection resulting from forest fires. Journal of Paleolimnology 28: 349-354.

Pratt, DW, RA Black, and BA Zamora. 1984. Buried viable seed in a ponderosa pine community. Canadian Journal of Botany 62: 44-52.

Precht, H, J Christophersen, H Hensel, and W Larcher. 1973. Temperature and life. Springer-Verlag, Heidelberg, Germany.

Qi, M, and JB Scarratt. 1998. Effect of harvesting method on seed bank dynamics in a boreal mixedwood forest in northwestern Ontario. Canadian Journal of Botany 76: 872-883.

Roberts, HA. 1981. Seed banks in soils. In: TH Coaker (ed.). Advances in Applied Biology, Volume VI. Academic Press, London.

Rowe, JS. 1983. Concepts of fire effects on plant individuals and species. In: RW Wein and DA Maclean (eds.). The role of fire in northern circumpolar ecosystems. John Wiley & Sons Ltd., New York.

Ryan, KC, and NV Noste. 1985. Evaluating prescribed fires. In JE Lotan, BM Kilgore, WC Fischer, and RW Mutch (technical co-coordinators). Proceedings, Symposium, and Workshop on Wilderness Fire. General Technical Report INT-182. USDA Forest Service. Intermountain Forest and Range Experiment Station. Ogden, UT.

Ryan, KC, and ED Reinhardt. 1988. Predicting postfire mortality of seven western conifers. Canadian Journal of Forest Research 18: 1291-1297.

Salter, J. 1857. On the vitality of seeds after prolonged submersion in the sea. Journal of the Linnean Society 1: 140-142.

Schafer, M, and PM Kotanen. 2003. The influence of soil moisture on losses of buried seeds to fungi. Acta Oecologica 24: 255-263.

Schimmel, J and A Granström. 1996. Fire severity and vegetation response in the boreal Swedish forest. Ecology 77: 1436-1450.

Shaukat, SS, and IA Siddiqui. 2004. Spatial pattern analysis of seeds of an arable soil seed bank and its relationship with above-ground vegetation in an arid region. Journal of Arid Environments 57: 311-327.

Staniforth, RJ, N Griller, C Lajzerowicz. 1998. Soil seed banks from coastal subarctic ecosystems of Bird Cove, Hudson Bay. Écoscience 5: 241-249.

Strickler, GS, and PJ Edgerton. 1976. Emergent seedlings from coniferous litter and soil in eastern Oregon. Ecology 57: 801-807.

Takahashi, K, and T Kamitani. 2004. Effect of dispersal capacity on forest plant migration at a landscape scale. Journal of Ecology 92: 778-785.

Telewski FW, JAD Zeevaart. 2002. The 120-yr period for Dr. Beal's seed viability experiment. American Journal of Botany 89: 1285-1288.

Ter Heerdt, GNJ, GL Verweij, RM Bekker, and JP Bakker. 1996. An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. Functional Ecology 10: 144-151.

Thomas, PA, and RW Wein. 1990. Jack pine establishment on ash from wood and organic soil. Canadian Journal of Forest Research 20: 1926-1932.

Thompson, K. 1986. Small-scale heterogeneity in the seed bank of an acidic grassland. Journal of Ecology 74: 733-738.

Thompson, K, and Grime, JP. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67: 893-921.

Timoney, KP, and G Peterson. 1996. Failure of natural regeneration after clearcut logging in Wood Buffalo National Park, Canada. Forest Ecology and Management 87: 89-105.

Tolonen, K. 1983. The post-glacial fire record. In: Wein, RW and Maclean, DA (eds.) The role of fire in northern circumpolar ecosystems. John Wiley & Sons Ltd., New York.

Turner, MG, WW Hargrove, RH Gardner, WH Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. Journal of Vegetation Science 5: 731-742.

Turner, MG, WL Baker, CJ Peterson, and RK Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1: 511-523.

United States Forest Service Fire Effects Information System database. 2005. http://www.fs.fed.us/database/feis/index.html.

Wang, GG. 2003. Early regeneration and growth dynamics of *Populus tremuloides* suckers in relation to fire severity. Canadian Journal of Forest Research 33: 1998-2006.

Warr, SJ, K Thompson, and M Kent. 1993. Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. Progress in Physical Geography 17: 329-247.

Whipple, SA. 1978. The relationship of buried, germinating seeds to vegetation in an old-growth Colorado subalpine forest. Canadian Journal of Botany 56: 1505-1509.

Whittle, CA, LC Duchesne, and T Needham. 1997. The importance of buried seeds and vegetative propagation in the development of postfire plant communities. Environmental Reviews 5: 79-87.

Yearsley, HK. 1993. Forest floor seed banks and their response to slashburning in some forest ecosystems in south central British Columbia. MSc thesis. University of British Columbia, Vancouver, BC. 136 pp.

Zasada, JC, RA Norum, RM Van Veldhuizen, CE Teutsch. 1983. Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce/feather moss stands in Alaska. Canadian Journal of Forest Research 13: 903-913.